2nd Quarterly Progress Report
Aug 28 - Nov 30, 1963
Contract NAS 2-1372

Biological Control Systems --A Critical Review and Evaluation

Vestibular Control System

This report is the second quarterly progress report under contract NAS 2-1372, "Biological Control Systems - A Critical Review and Evaluation", covering work carried out during the period 28 August , 1963 to 30 November, 1963.

The first report dealt with the organization and aims of the study and an outline of the method of review and analysis to be applied to each biological control system. It also included the introductory chapter on defining biological control systems, which discussed in detail many of the characteristics of biological systems which are not usually found in conventional servomechanisms.

During the second quarter, over one hundred papers were reviewed in the fields of visual, manual, and vestibular control systems. The technical portion of this report will present the vestibular system as a biological control system, integrating the contributions from the fields of psychology, physiology, anatomy, aviation medicine and engineering. This will be followed by a lengthy bibliography covering most of the literature relevant to the non-clinical aspects of the vestibular system.

Finally, reviews and critiques of many of these papers are included to show the type of work presented in some of the representative articles in the field.

In the next quarter we plan to concentrate on review and evaluation of the manual control literature. Since this is the

field which has received more attention than any other biological control system, the review should be concerned primarily with sorting and selecting the important results, rather than searching for relevant material.

As of the end of the second quarter, it is estimated that the work is 49 % completed.

Progress Report No. 2 on NAS 2-1372

August 28 - November 30, 1963

Biological Control Systems - A Critical Review and Evaluation.

VESTIBULAR CONTROL SYSTEM

I. DEFINITION OF CONTROL VARIABLES.

The vestibular control system in man is one of several systems used to determine his orientation in space. As a single channel of a multi-input control system (other inputs including visual, aural, tactile and kinesthetic sensations), it is particularly difficult to specify its dynamic characteristics without careful consideration of the other inputs. It is possible, nevertheless, to define a set of inputs and outputs for the vestibular system as if it acted alone.

The vestibular system in man is the nonauditory labyrinth in each inner ear, consisting of sets of semicircular canals and otoliths. The three semicircular canals, oriented in roughly orthogonal planes, respond to angular acceleration about an axis normal to the plane of the canal. The otoliths are stimulated by linear acceleration as well as the gravity field, similar to three-axis accelerometers. They are actually specific force receivers. (Specific force is the gravity vector minus the linear acceleration vector.)

Since the orientation of the inner ear does not change with respect to the head, we may refer all accelerations to motion of the head. Thus the inputs to the vestibular system are two vector quantities --angular acceleration sensed by the canals and the specific force sensed by the otoliths.

Identification of the output also requires careful consideration. An engineer familiar with inertial navigation systems is tempted to draw the analogy, with the semicircular canals providing the attitude signals usually generated by gyroscopes, and the otoliths providing the linear acceleration signals to be twice integrated, yielding position. Attractive as this speculation may be, there is not evidence that man uses these inertial senses for navigation (10). One of the vestibular outputs is a "component" of the perceived orientation in space. Although it is not usual to refer to a perceived quantity as an output of a control system, it is nevertheless true that in the case of the vestibular system, the subjective feeling man receives about his orientation and movement with respect to an outside reference is an important output. This perceived orientation may be drawn out as an explicit and measureable signal by any of several methods. Simple subjective reports, such as, "I am rotating to the left", or "I am tilted backwards", yield crude information about the direction and time duration of perceived orientation changes. A second class of measurement of changes in perceived orientation uses the well-known techniques of psychophysical quantitization of sub-

jective feelings. These tests rely upon the ability of a subject to adjust some measureable physical parameter until it exactly matches his subjective perception of his orientation. The third category of testing the perceived orientation involves tests of the ability of man to control his orientation in a closed loop control system, in which his vestibular system serves as error sensor.

The block diagram representation of the vestibular control system shown in Fig. 1 represents the labyrinthine system from a "black box" point of view as discussed above. The specific force vector $\bar{f}$, and the angular acceleration vector $(\dot{\omega}_{IA})$ (rate of change of angular velocity of the head with respect to inertial space) are the two inputs. The projection of these vector inputs on the semicircular canals and the otoliths are determined by the orientation of these elements in the head and the instantaneous orientation of the head with respect to inertial space. The matrix $[A]$ represents the appropriate linear transformation from an inertially fixed frame of reference to the frame of reference fixed with respect to the subject's head. The output f_b corresponds to the component of specific force along a hypothetical input axis of the otolith, and similarly $(\dot{\omega}_{IA})_b$ represents the component of angular acceleration along the input axis of each semicircular canal. These angular and linear acceleration components are then multiplied by the sensitivity of the otoliths and canals and acted upon by the dynamic response of these organs. Nonlinearities

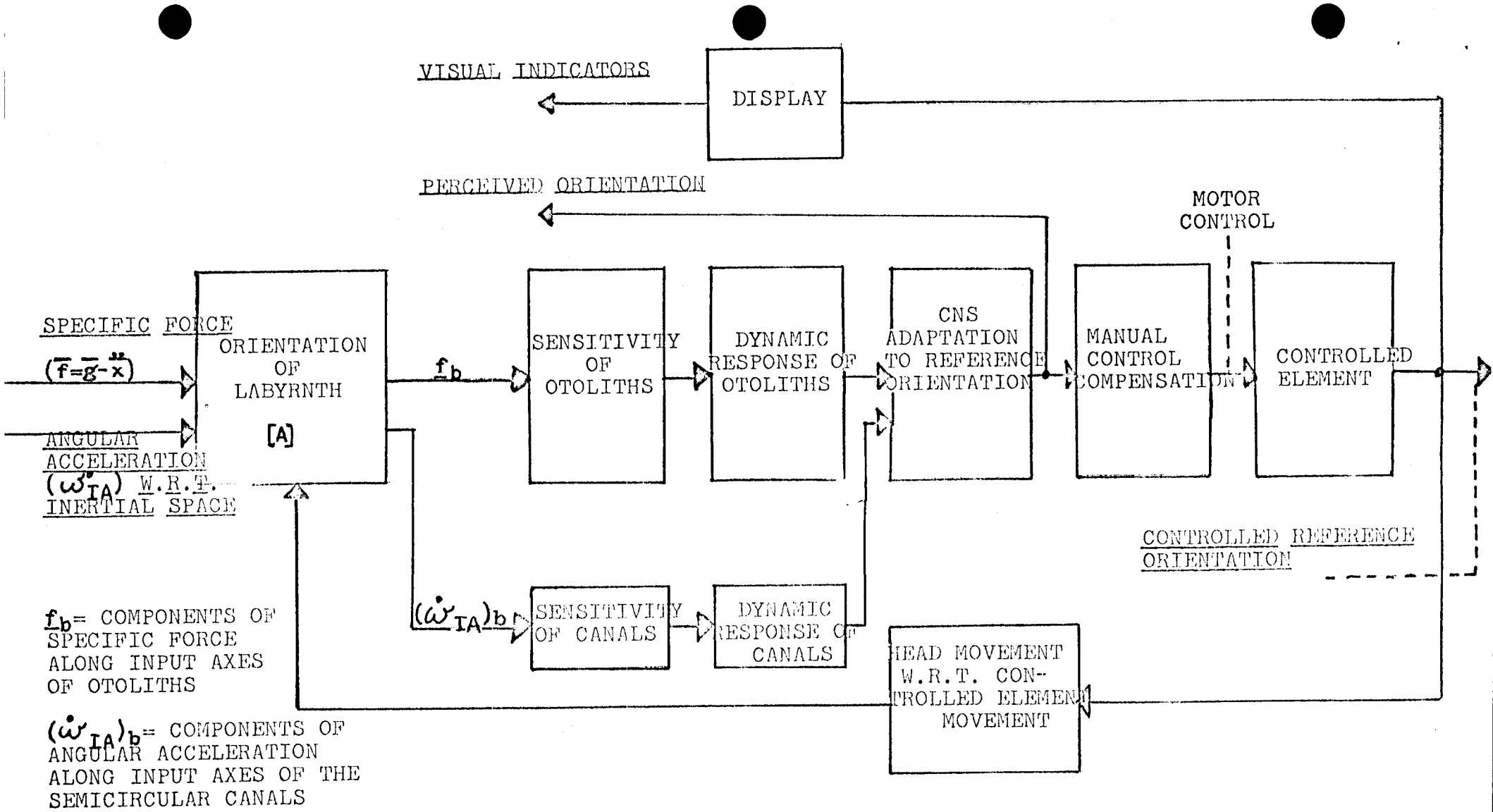


FIG. 1. BLOCK REPRESENTATION OF THE VESTIBULAR CONTROL SYSTEM

in the organs may be included in the block representation of their sensitivity. The central nervous system is shown to combine the outputs of the otoliths and canals, as well as possible visual, aural, tactile or kinesthetic sensation, to compose a perceived orientation of the man in space. Any adaptation to a new reference orientation in space which cannot be assigned to the sensitivity of dynamic response of the otoliths and canals is arbitrarily assigned to the function of the central nervous system.

An additional output of the vestibular system is the set of control signals sent to the extra-ocular muscles. It is well-known that the vestibular system, when stimulated, drives the eyes conjugately in the direction opposite to perceived rotation, thereby tending to stabilize the eyes in space despite rotations of the head. The importance of optokinetic nystagmus as an indicator of vestibular function will be discussed in detail later in this report.

When the vestibular sense is used for closed loop control, as in riding a bicycle, flying an airplane, or walking a tightrope, it leads directly to manual control compensation by turning a control wheel or adjusting one's weight for better balance. The resulting motor control output can be measured as an additional indicator of the vestibular function. When the manual response is processed through the control dynamics of the controlled element, it results in a change in the orientation of the controlled element, i.e., the attitude of the airplane or the tilt of the bicycle.

For closed loop representation of the functioning of the vestibular control system, the output may be considered as the controlled reference orientation. Feedback to the vestibular system occurs as the orientation of the head in space varies as a direct result of the change in controlled reference orientation.

A great deal of the experimental and theoretical investigations of the vestibular system have been concerned with the normal and abnormal functioning of the portion of the block diagram from input acceleration to the output as perceived orientation or vestibular nystagmus. In its normal operation in man's daily experience the vestibular system serves as an integral part of a closed loop control system through some external controlled element, which may be no more complex than his own postural control system or may involve control of complex vehicles.

In the following sections, we will review and evaluate various studies which bear on the makeup of the boxes shown in this general block diagram. In particular we will deal with the anatomy and physiology of the system, behavioral data relating to primarily psychological observations on its normal functioning, results of linear and nonlinear control system identification attempts to describe the vestibular system, and discussion of the attempted control theory models for its operation. We will conclude with a suggestion of possible further experimental and analytical programs which might uncover some of the hidden aspects of this biological control system.

II ANATOMY AND PHYSIOLOGY

The vestibular apparatus, comprising the nonauditory portion of the labyrinth in the inner ear, consists of two major portions: the semicircular canals and the vestibule. Fig.2 shows the structural arrangement of the vestibular apparatus and Fig.3 presents a simplified drawing of the important functional members.

The semi-circular canals, three on each side of the head, lie in planes which are nearly mutually orthogonal, and permit angular accelerations about any axis to be sensed. The horizontal canals lie in a plane tilted up in front by about 25-30° from the actual horizontal. The entire vestibular apparatus is filled with endolymph fluid with density and viscosity close to that of water.

Each canal starts from a common sac called the utricle, forms roughly a semicircle, and returns to the other end of the utricle. Near the utricle each canal has an enlarged region called the ampulla, in which the sensory elements are located. Fig.4, a cross section of an ampulla, shows that is is nearly entirely sealed by the cupula and crista. The cupula, which is a gelatinous substance of the same density as the endolymph, is displaced by movement of the fluid in the canal. The cupula lies above the crista, a rigid sensory cell formation, and is imbedded with cilia - hair-like sensory cell endings from the crista which sense displacements of the cupula. The crista is supplied with approximately 20,000 nerve fibers to transmit vestibular information to the brain.

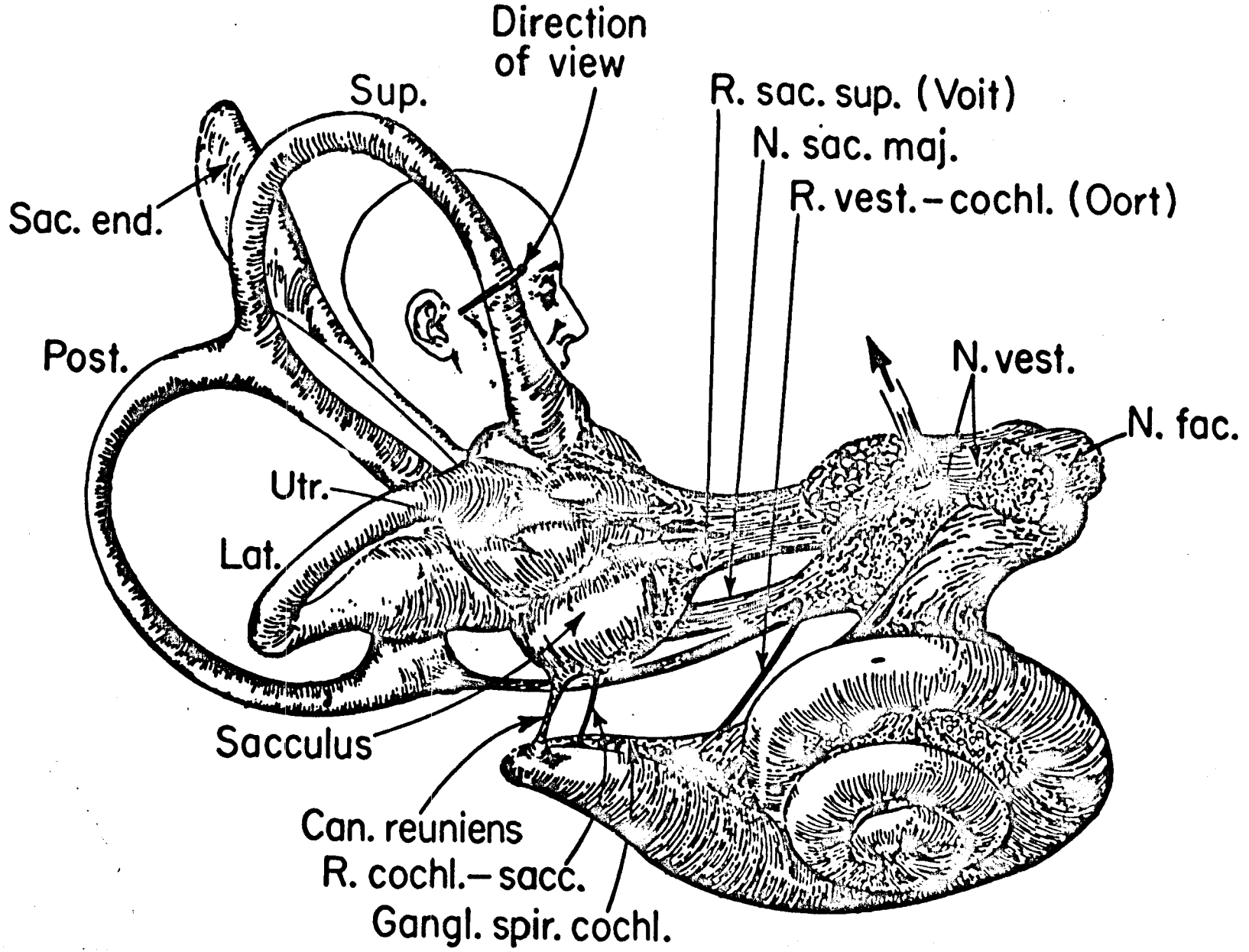


Fig. 2. The vestibular apparatus, cochlea, and structural relations of innervation of human labyrinth. (ref. [illegible])

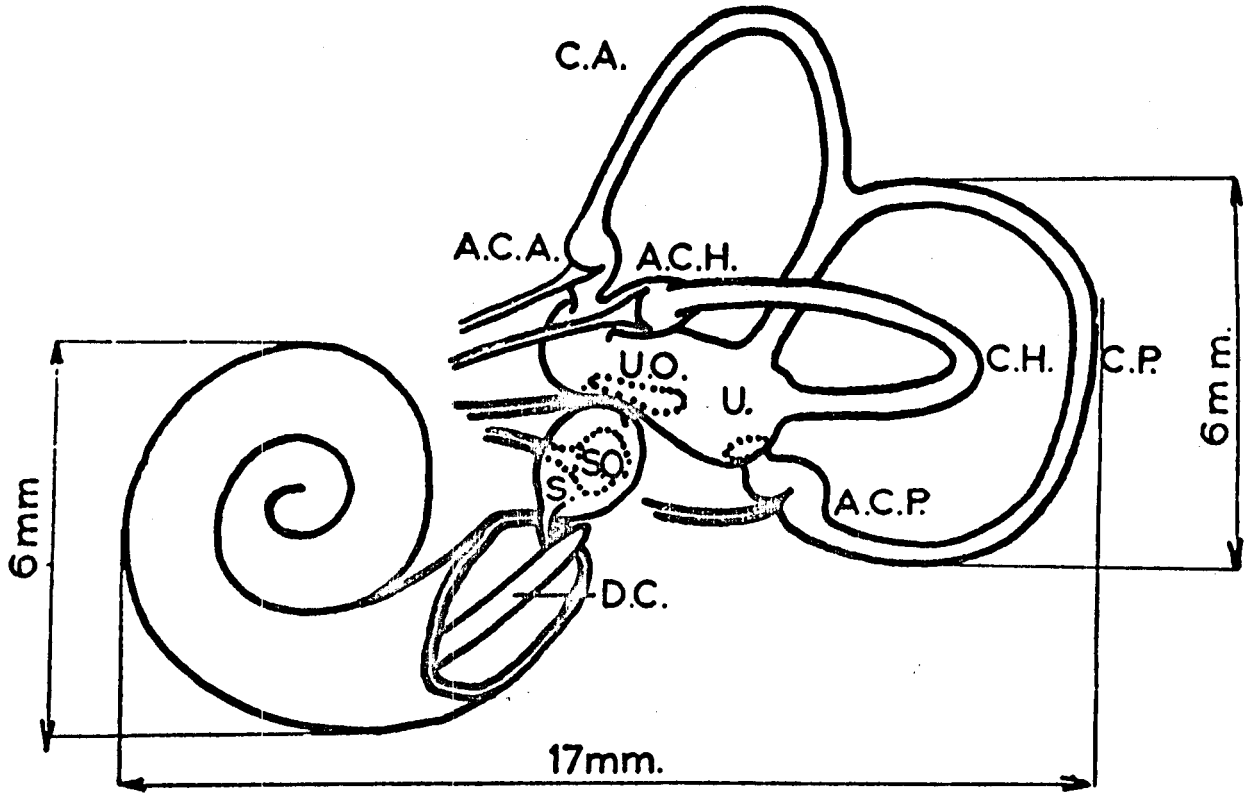


Fig. 3. Ventro-lateral view of the left human labyrinth.

A., A.C.H., A.C.P., ampullae of anterior, horizontal and posterior canal. C.A., C.H., C.P., anterior, horizontal and posterior canal. D.C., cochlear duct. S. and S.O., saccule and its otolith. U. and U.O., utricule and its otolith. (ref. 73.)

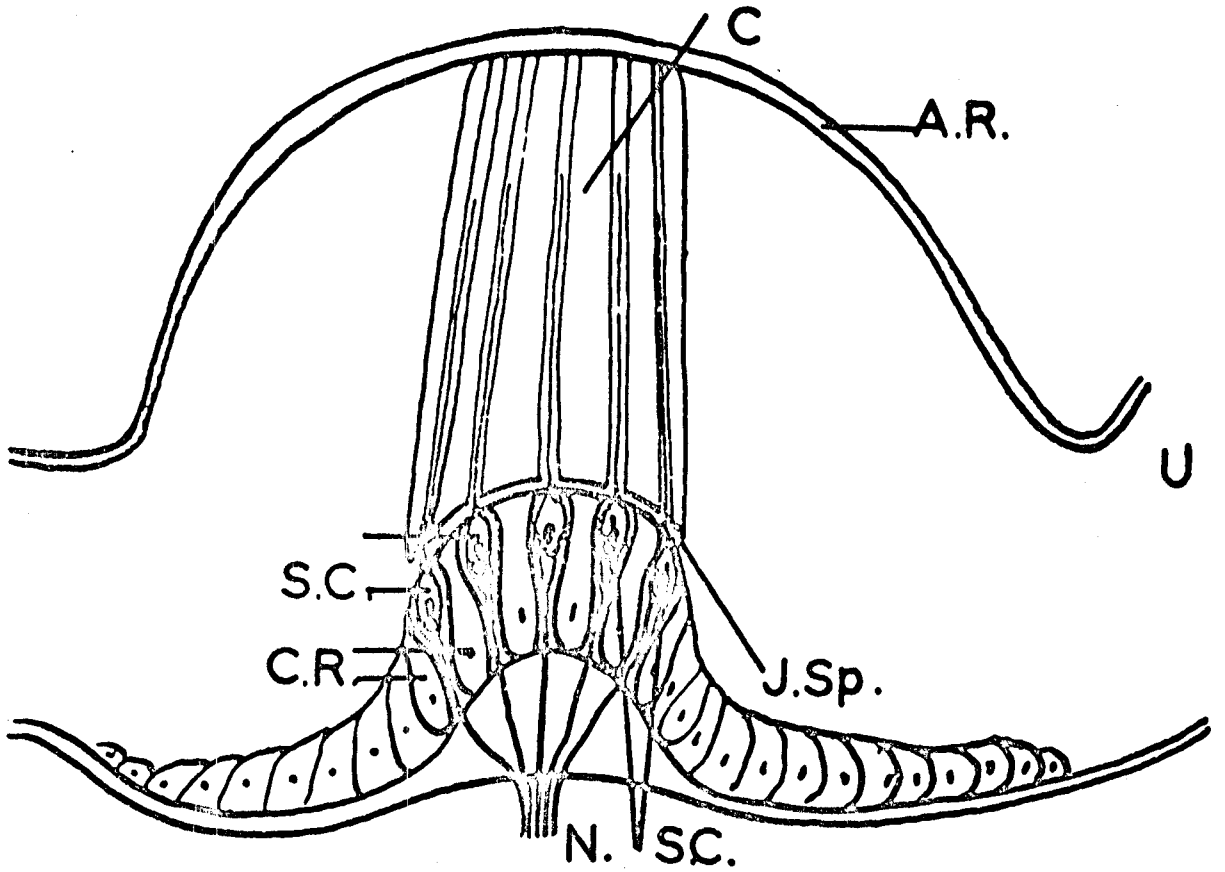


Fig. 4.

Schematic drawing of a cross section through an ampulla, with cupula and crista. A.R., ampulla roof. C.R., crista, consisting of S.C. (sensory cells), supporting cells and N. (nerve fibres). Between cupula and crista there is the I.S.P. (intercupular space). U., utricule. (ref. 73)

The cupula hermetically seals the ampulla. When the angular acceleration of the head causes the endolymph fluid to lag behind the structure in a canal,(inertial reaction forces), the cupula is displaced from its normal position. The displaced cupula has its position transmitted through the crista, over which it can be moved, and also exerts an elastic restoring force on the fluid.

Since the cupula is of the same density as the endolymph it is perfectly floated, and therefore does not bend under gravitational force or linear acceleration.

The vestibule, forming the other major portion of the vestibular system, consists of two fluid filled sacs, the utricle and the saccule. Each of these sacs contains an otolith (literally ear stone), a heavy gelatinous mass containing calcium carbonate crystals and resting on the sensory macula. (See Fig. 5) The utricle otolith and macula are roughly horizontal, and the saccule sensors perpendicular.

Under the action of specific force (gravity or linear acceleration) the heavier otoliths tend to move through the less dense fluid in the direction of the force. The otolith slides across the macula, restrained by supporting strands which limit its movement to about 0.1 mm. Just as in the case of the crista and cupula, the macula containing sensory cells has cilia imbedded in the otolith. These cilia are pushed or pulled as the otolith moves in response to specific force, and transmit this information through the macula to the brain by means of the shear force they exert on the sensory cells. The otoliths are sensitive to changes in magnitude as well as direction of specific force.

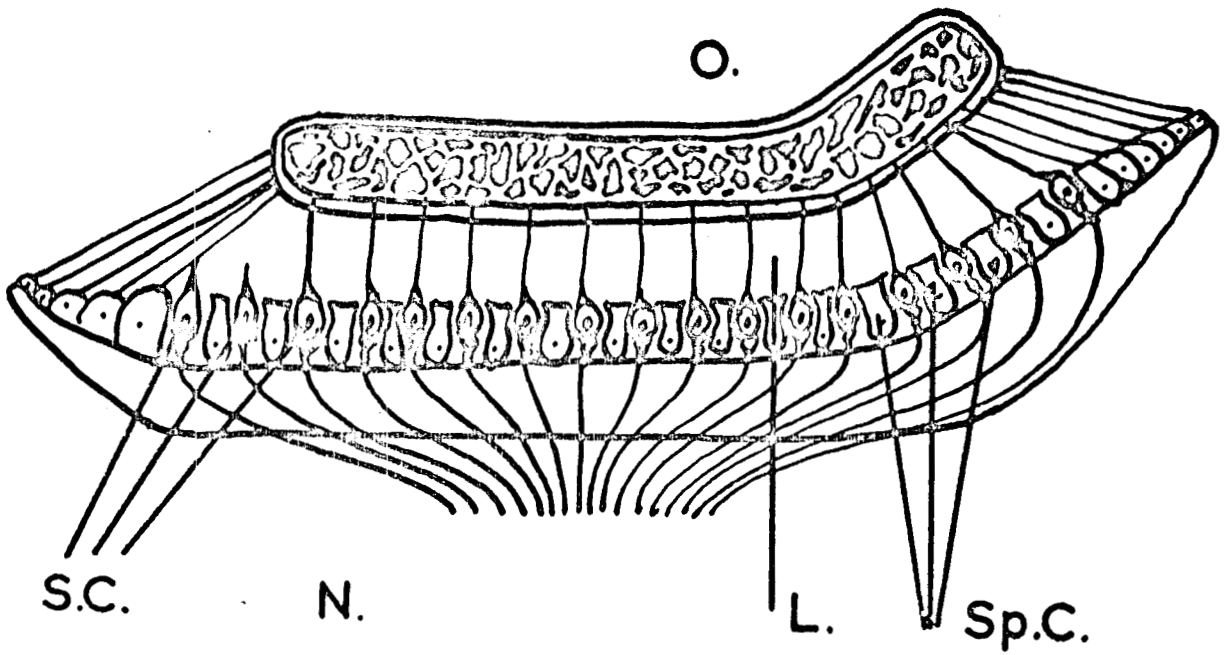


Fig. 5.

Schematic drawing of a cross section of an otolith and its macula. O. is the otolith, suspended by strands which run from the margins to the macula, consisting of supporting cells (Sp.c.) and sensory cells S.C. Between the otolith and the macula there is a thin layer (L.) to allow the otolith to slide over the macula. N. is the nerve. (ref. 73)

Coding of information from the vestibular sense organs is of an FM nature. In the normal position of the otolith or cupula the neural message is a resting discharge rate of action potentials. Shifting the otolith in one direction increases the discharge rate, and in the other direction decreases the frequency. Detailed studies of this mechanism have been conducted in the ray fi .

For small deflections around the normal position of the cupula the change in discharge frequency is roughly proportional to the displacement. Naturally the frequency cannot decrease below zero - leading to a saturation in one direction for each canal corresponding to a cupula deflection of the order of 30^{o}.

In addition to the nerve fibres which fire at a rate dependent on position, another type of receptor has been observed in the otolith sensory cells. These receptors are sensitive only to changes in otolith position, and decrease to zero actively when the otolith assumes a new steady-state position. These rate receptors are located near the borders of the macula, with the position receptors occupying the central regions. No such rate sensitive receptors have been discovered in the semicircular canals.

The actions of the vestibular mechanisms on the two sides of the head are synergetic - with the activity levels from both sides compared before a single resultant signal is transmitted up the central nervous system. Thus the traumatic loss of one labyrinth causes disorientation which is partially compensated in a period of one year.

III. BEHAVIORAL EXPERIMENTAL RESULTS RELATING TO THE VESTIBULAR CONTROL SYSTEM

The vestibular mechanism plays a varied role in controlling man's actions in his daily activities. The major behavioral implications of its role are reviewed in this section.

Postural Control:

The otoliths, and particularly the utricle, are the chief source of non-visual information to the postural control system. They sense the direction of the apparent vertical and control muscular tone of the arms, legs, and neck, etc. to counter the gravitational force and avoid falling over. (When available, visual and tactile cues also provide inputs to the postural control system.) Experiments indicate the inability of cats to right themselves when dropped from an inverted position in the absence of visual cues and after denervation of the utricula macula.

Since the semicircular canals are not affected by linear acceleration, they can serve no role in postural control against the force of gravity. The weight of internal organs apparently does not provide important cues for the regulation of muscle tone.

Compensatory Eye Movements:

When the skull is rotated in space the vestibular apparatus acts to stabilize the eyes with respect to the outside environment and thereby stabilize the image of a

stationary point on the retina. It does this by moving the eyes slowly in the direction opposite to the movement, apparently without any initial delay. Since the eyes cannot continue to rotate, after reaching a certain deviation from their central position a fast return phase occurs. The combination of this slow sweep and fast return is known as vestibular nystagmus. Use of this nystagmus as an indicator of vestibular sensation is discussed at length in the next section.

Illusions Attributed to the Vestibular System:

Since the vestibular system forms one of the important inputs to the human perception of his orientation it may be expected that bizarre stimulation of the vestibular system should yield strange illusions of movement. When these illusions lead to spatial disorientation by a pilot they are of an exceedingly serious nature (32). Nuttall (133) refers to a study which attributes 14% of fatal aircraft accidents to spatial disorientation. Krauss (103) reports "when there is a conflict between the instruments and normal sensory mechanisms, the flight student is very likely to revert to the use of the sensory cues which he has been using all of his life". The most common illusions are reviewed briefly by Fogel (187). He includes descriptions of the visual-g illusion, the autokinetic illusion, the oculogyral illusion, the oculogravic illusion, the non-visual illusion, and the audiogyral illusion. In those in which the vestibular apparatus plays a part, the illusion may be explained

in terms of misinterpretation of vestibular sensation, often because of a failure to realize what the orientation or acceleration of the aircraft actually is. When such illusions result in the subjective loss or orientation with respect to the direction of vertical, pilots are said to have vertigo.

Vestibular Stimulation and Motion Sickness:

There is no question that motion sickness may be caused by certain patterns of acceleration sensed by the semicircular canals and otoliths. (Destruction of the labyrinth eliminates susceptibility to motion sickness.) There is also general agreement that motion sickness is more likely during a conflict between visual and non-visual senses of orientation (as in an airplane) than when the two agree. Other factors which are supposedly contributory include odor, temperature, size of the enclosure, repeatability of the motion, disagreeable sights, distasteful food, suggestion of sickness by others, training and adaptability, warning of the motions to expect, and, perhaps most important, individual susceptibility to motion sickness.

For investigators interested in the control characteristics of the vestibular system a study of the conditions leading to motion sickness might appear fruitful as indications of the inability of the system to give suitable information on body motion. Despite a great deal of careful research, incidental observations and anecdotal information, very little has been

established about the etiology of motion sickness. There is no agreement, for example, on whether linear or angular acceleration (or both) contribute to motion sickness and vomiting. The state of knowledge about motion sickness is revealed in the proceedings of a symposium held in 1960 to which ten experts contributed. (Symposium in Motion Sickness with Special Reference to Weightlessness - 6570th Aerospace Medical Res. Lab. USAF-WPAFB- Tech. Documentary Report AMRL-TDR-63-25-June 1963.) In his summary statement the symposium moderator states, "there is a feeling that this is a very complex situation in which there are a number of uncontrolled variables of undetermined importance".

At the present time there seems to be very little to be learned about the control characteristics of the vestibular system from a study of motion sickness.

IV. CONTROL SYSTEM DESCRIPTIONS AND EXPERIMENTS RELATING TO THE VESTIBULAR SYSTEM

This section deals with those experimental results and models which have direct relevance to a control system description of the vestibular mechanism. The results are divided into two groups; those bearing primarily on the semicircular canal system and those pertaining primarily to the otoliths. It will be seen that a wealth of carefully compiled experimental material exists for evaluation of models of the semicircular canals. The lack of careful experimental data on otolith performance reflects the greatly increased difficulty of performing unambiguous experiments on the otoliths.

SEMICIRCULAR CANALS

Historical:

The development of current theories of the operation of the semicircular canals dates from the work of Steinhausen (160), who suggested that the operation of each semicircular canal may be viewed as the mechanical action of a torsion pendulum. The moment of inertia of such a pendulum corresponds to the moment of inertia of the fluid ring in the semicircular canal, the damping term results from the viscous forces as the endolymph flows through the narrow canal, and the elastic restraining force is attributed to the cupula, which is displaced from its neutral position by any movement of the endolymph in the canal. By showing that the cupula seals the ampulla nearly entirely, not permitting free steady

state flow of the endolymph, Steinhausen dismissed the concept of the canal as a leak canal and strengthened the plausibility of a torsion pendulum model. The measurement of suitable output variables to test the validity of this model in man posed a great difficulty at first and Steinhausen suggested that the time of occurrence and disappearance of subjective feelings of rotation should be correlated with a minimum threshold deviation of the cupula.

The earliest experimental attempts to ascertain the parameters of the second order equation proposed by Steinhausen were carried out by Van Egmond, Groen& Jongkees, at Utrecht.[16] Their schematic diagram of the semicircular canal is shown in Fig. 6.

The differential equation for the angular deviation of the endolymph in relation to the skull, and therefore the presumed angular deviation of the cupula is given by:

$$\Theta \ddot{\xi} + T \dot{\xi} + \Delta \xi = \alpha \Theta$$

where Θ = moment of inertia of the endolymph,

T = moment of friction at unit angular velocity of the endolymph with respect to the skull,

Δ = stiffness, or torque moment per unit angular deflection of the cupula (ξ),

ξ = angular deviation of the endolymph with respect to the skull,

$\dot{\xi}$ = angular velocity of the endolymph with respect to the skull,

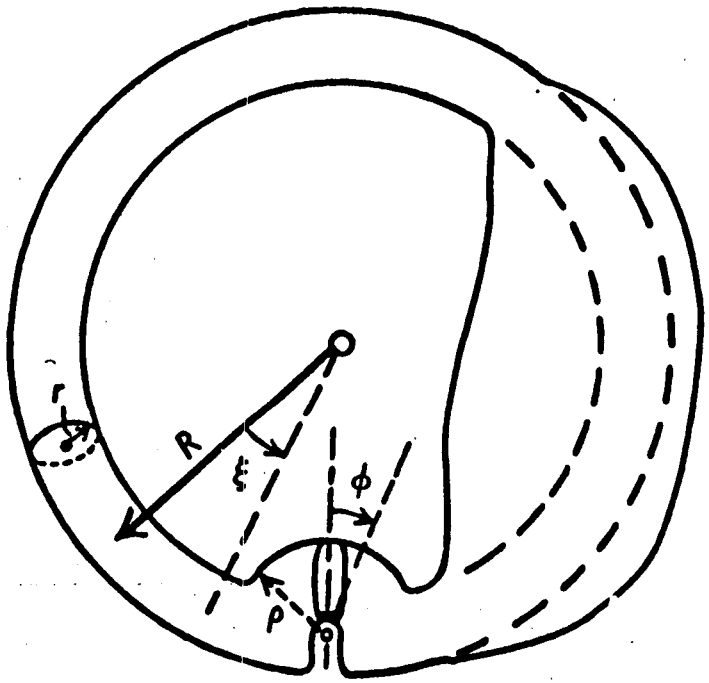


Fig. 6. Schematic diagram of the semicircular canal. When the endolymph moves over an angle of ξ the cupula is forced over an angle of ϕ; ξ and ϕ are of the same order of magnitude. (ref. 165)

$\ddot{\xi}$ = angular acceleration of the endolymph with respect to the skull,

α = component of angular acceleration of the skull, with respect to inertial space, normal to the plane of the semicircular canal.

The dynamic response of this model is completely determined by two parameters, π/θ and Δ/θ. Most of the experimental results to be reviewed in this section relate to determinations of these constants by indirect methods.

Theoretical Determination of π/θ :

An approximate value for the ratio of the friction coefficient to the moment of inertia may be calculated from anatomical data on the semicircular canals (165). Assuming that the mass of endolymph which must be moved includes an effective continuation of the semicircular canal through the whole circle in the utricle, its moment of inertia is given by:

$$\theta = 2\sigma\pi^2 r^2 R^3$$

where R = radius of the canal,

σ = density of the endolymph,

r = circular cross section radius of the canal.

In calculating the value of π, it is assumed that significant frictional moments exist in the narrow portion of the canal but not in the utricle, and therefore only half the circumference of the circle, πr is considered. Application of

Poiseuille's Law to this situation yields:

$$\pi = 8\eta\pi^2 R^3$$

where η = the viscosity of the endolymph.

The ratio π/θ is therefore independent of R, and given by:

$$\pi/\theta = 4\eta/\sigma r^2$$

Use of the values $\eta = 0.006$ (grams/cm/sec), r = 0.03 cm, and $\sigma = 1.0$ grams/cm^3 yields the approximate value ratio of:

$$\pi/\theta \approx 27 \sec^{-1}$$

Theoretical determination of the value of Δ/θ, would presuppose a knowledge of the elasticity or spring restraining force of the cupula when deflected by the endolymph. Since such information has never been obtained, no theoretical estimate of this parameter may be offered. Based on indirect evidence, however, the value of Δ/π appears consistently to yield a level of approximately 0.1 sec^{-1}. Considered with the estimate of π/θ given above, this would yield a value:

$$\Delta/\theta \approx 2.7 \sec^{-2}.$$

Experimental Determination of Torsion Pendulum Parameters:

<u>Duration of Post-Rotation Sensation</u>: The roots of the basic torsion pendulum equation are given by:

$$\omega_{1,2} = \frac{-\pi \pm \sqrt{(\pi^2 - 4\Delta\theta)}}{2\theta}$$

Since the system is very highly damped (the quantity under the square root sign is positive and much greater than one) the

roots are widely separated, yielding one very short and one very long time constant. Assuming $\Delta/\pi \ll \pi/\theta$, the roots are:

$$\omega_1 \approx -\Delta/\pi$$
$$\omega_2 \approx -\pi/\theta$$

In Laplace transform notation the relationship at cupula position to head acceleration is:

$$\frac{\xi(s)}{\alpha(s)} = \frac{1}{\theta}\left[\frac{1}{(s+\Delta/\pi)(s+\pi/\theta)}\right]$$

Consider what would happen to the cupula if the skull were suddenly brought to a stop after steady state rotation at constant velocity γ rad/sec. Solution of the equation with initial conditions $\xi = 0$ and $\dot{\xi} = \gamma$ yield:

$$\xi = \gamma\frac{\theta}{\pi}\left(e^{-\frac{\Delta}{\pi}t} - e^{-\frac{\pi}{\theta}t}\right)$$

The resulting deviation is plotted in Fig. 7 where the slow exponential decay appears as a straight line on a plot of log cupula deflection versus time. The physical interpretation of this movement is as follows: Following the sudden stopping of the skull, the angular momentum of the fluid carries it past the zero position with initial velocity γ, and it is slowed to a stop by the friction of the endolymph in the canal; the endolymph and cupula each reaching a maximum deflection. $\left(\xi_{max} \approx \gamma\theta/\pi\right)$ Time constant for this fast deflection of the cupula is approximately θ/π. Following this maximum deflection the weak elastic force of the cupula slowly forces

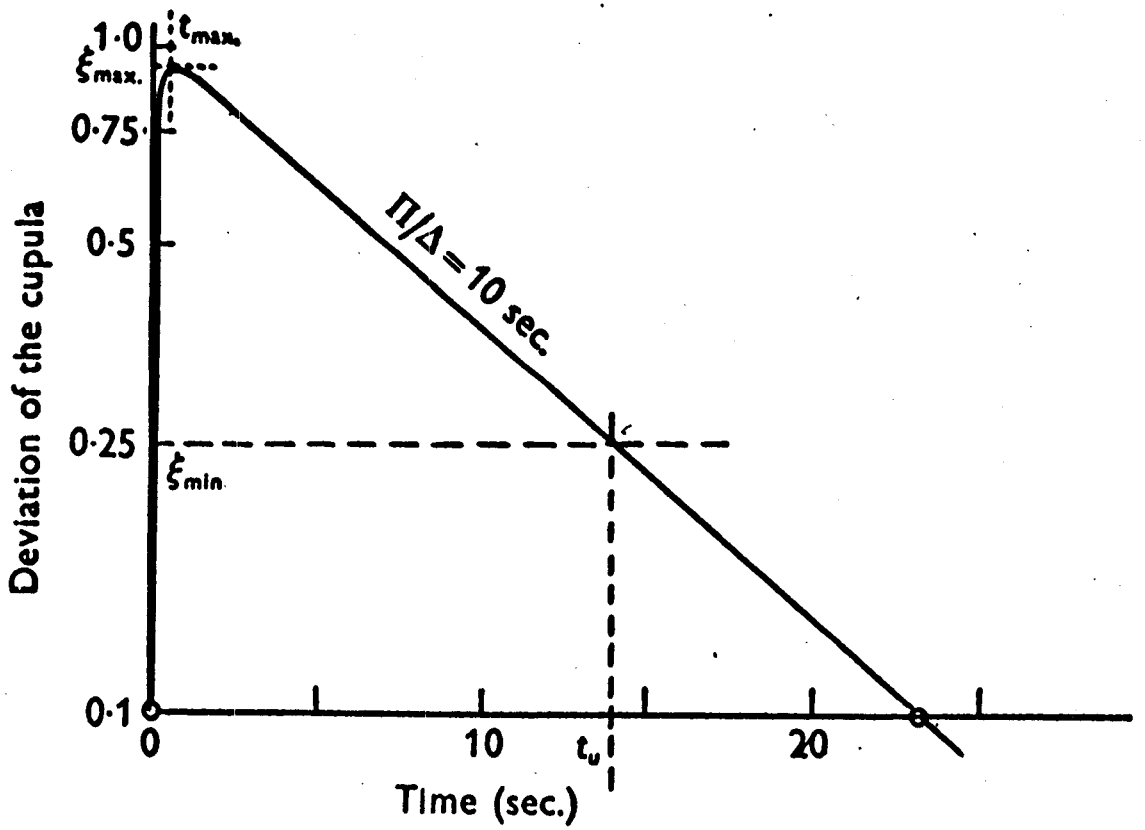


Fig. 7. Deviation ξ of the cupula produced by sudden arrest of an angular velocity $\gamma°$/sec. Maximum deviation at $t = 0{\cdot}5$ sec.; minimum deviation passed at $t = 14$ sec., giving rise to sensation. Ordinate logarithmic. Slope of curve gives Π/Δ. (ref. 165)

the endolymph to return to its initial position, opposed chiefly by the friction force. During this period the system resembles a simple first order system, and exhibits exponential decay:

$$\xi = \gamma \frac{\Theta}{\pi} \left(1 - e^{-\frac{\Delta}{\pi} t}\right)$$

To make use of this hypothetical relationship for tests of the torsion pendulum parameter, van Egmond, et al. assumed the threshold of subjective sensitivity to rotation is equivalent to a specific angular deviation of the cupula ξ_{min}. Whenever the cupula deflection exceeds this value the subject should report the sensation of rotation. The curve of Fig. 7 shows that the time duration from the stopping of the actual rotation until the cupula falls below its threshold level ξ_{min} is dependent upon the original angular velocity of the subject.

$$t_4 \approx \frac{\pi}{\Delta} \log \left(\frac{\Theta \gamma}{\pi \xi_{min}}\right)$$

This equation indicates that the duration of the sensation of rotation should be proportional to the logarithm of the initial angular velocity. Tests to determine this relationship are known as cupulograms, and a typical example is shown by the line marked "sensation" in Fig. 8. The relationship between time duration and the initial angular velocity (called the impulse) is indeed approximately logarithmic. According to the above equation the slope of the cupulogram should yield

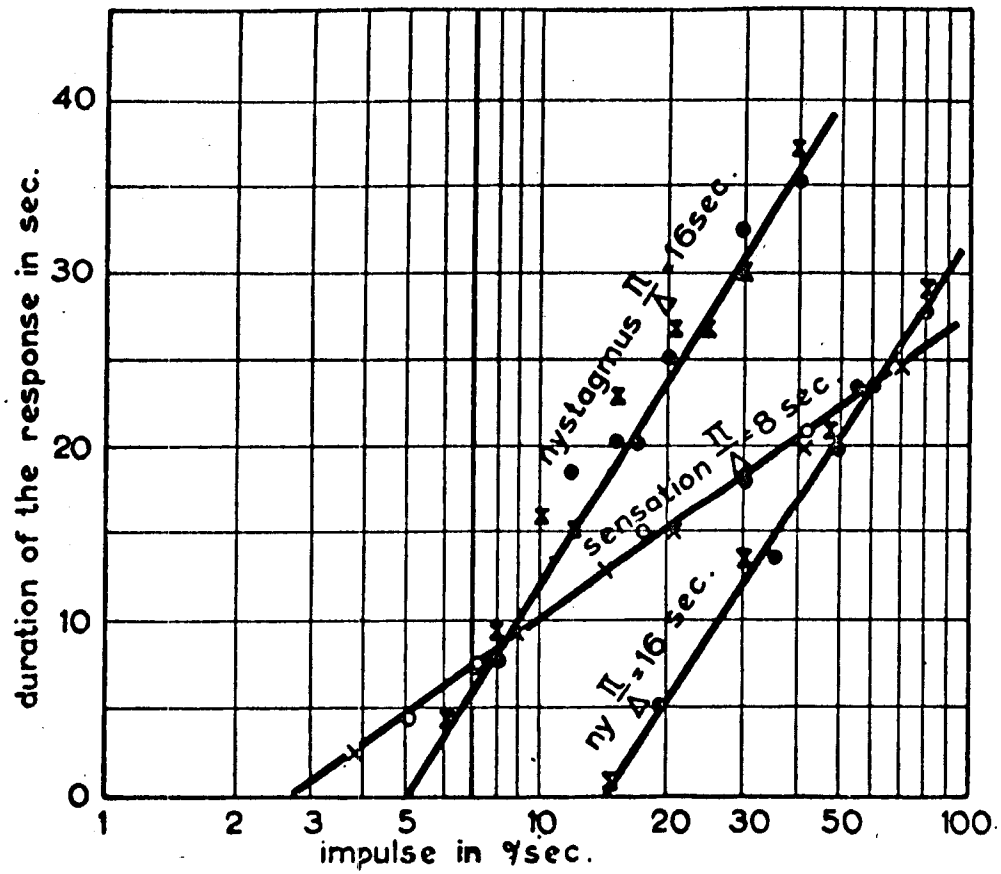


Fig. 8. Normal cupulograms of sensation and nystagmus. Depending on the observer's skill, the nystagmus threshold will be localized between 5 and 15°/sec; the steepness of the nystagmus cupulograms should stay the same.

O clockwise rotation
X counter clockwise
} sensation ● } idem for nystagmus. (ref. 73)

the value of π/Δ. For the line given in Fig. 8, π/Δ = 8 sec., which is about the average found for all normal subjects tested. The average minimum impulse that leads to any sensation of post-rotation is γ_{min} = 2.5 degrees/sec.

Step Response to Acceleration: The cupulogram discussed above is based on the time necessary for the cupula to return to the threshold level and indicate a cessation of the sensation of rotation. If the subject is started from rest and rotated at a constant acceleration α rad/sec^2, the angular deviation of the cupula should be:

$$\xi \approx \alpha \frac{\theta}{\Delta}(1 - e^{-\Delta t/\pi})$$

This time course is shown in Fig. 9. The subject will first sense rotation when his cupula deviation reaches ξ_{min}, which occurs after a latency of τ seconds. For small values of τ compared with π/Δ,

$$\xi_{min} = \alpha \frac{\theta}{\pi} \tau \quad \text{or}$$

$$\alpha\tau = \xi_{min} \frac{\pi}{\theta}$$

The prediction would be that the product $\alpha\tau$, which van Egmond et al. call the "Mulder" product should remain constant. Their results show it approximately constant (1.5 - 2.0 degrees/sec.) over angular accelerations from 1 - 5 degrees/sec^2. Moreover, this Mulder product which indicates the integrated acceleration necessary to force the cupula over to its threshold level, should just be equal to γ_{min}, the threshold level of initial impulse found from

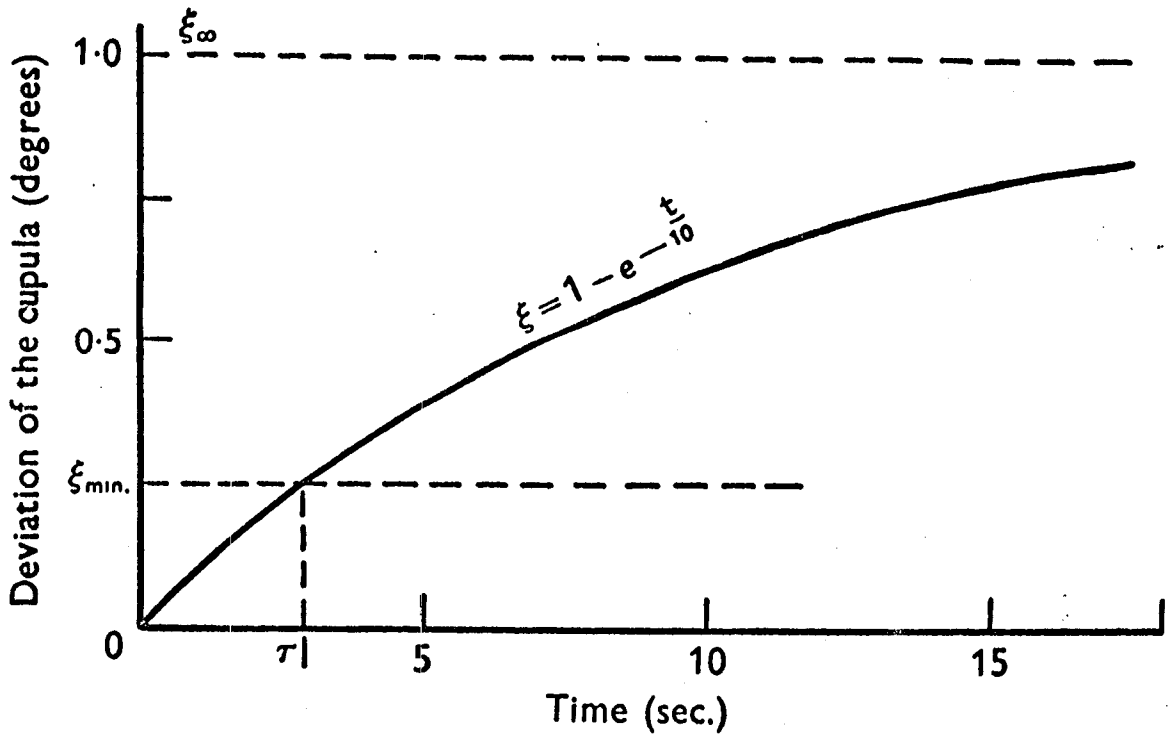


Fig. 9. Deviation ξ of the cupula under influence of a constant angular acceleration $(1°/sec.)^2$. The latent period τ seconds lies between start and the moment when the cupula passes $\xi_{min.}$. After infinite time (about 30 sec. in practice) the cupula attains equilibrium. (ref. 165)

the cupulogram experiment. That value (γ_{min} = 2.5 degrees/sec) is in fairly good agreement.

Sinusoidal Stimulation: By rotating the subject about a vertical axis on a torsion swing the skull could be forced to undergo sinusoidal accelerations of instantaneous value $\propto \sin \omega t$. The second order system model for the semicircular canal predicts that ξ should be in phase with the acceleration at very low frequencies, lagging the acceleration input by 90 degrees at the undamped natural frequency ($\omega_o = \sqrt{A/\Theta}$) and finally lagging input acceleration by close to 180 degrees at very high frequencies. By determining the subjective resonance or 90 degree phase lag point, one can estimate the value of ω_o. At the resonance frequency the cupula acts as a pure velocity meter, and would indicate to the subject that he is at rest (zero velocity) only at the peaks of his swings on the torsion pendulum. Van Egmond et al. find an average value of 1 rad/sec for the natural frequency, thus:

$$A/\Theta = 1.0 \text{ sec}^{-2}$$

They estimate the probable error in A/Θ as about 20% and that in π/Θ as about 25%.

The torsion swing experiments yield another method of checking the level of ξ_{min}, the threshold displacement of the cupula. As the torsion swing vibrations gradually decrease in amplitude the test subject will find his sensation decreasing until he senses only the maximum point on the swings (see Fig. 10).

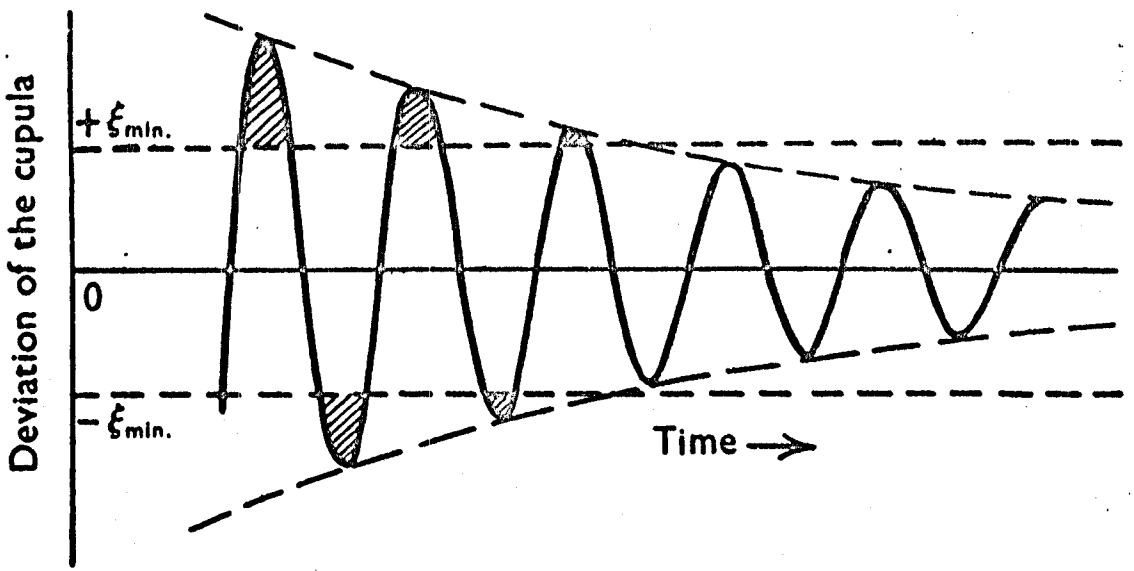


Fig. 10. Deviation of the cupula on the torsion swing in the neighbourhood of the minimum. Only the tops of the declining sine wave are associated with sensation. (ref. 165)

Assuming a value of acceleration α_{min} at a frequency ω to just reach threshold, the cupula equation gives a threshold level of cupula displacement as:

$$\xi_{min} = \frac{\alpha_{min}}{\omega} \frac{\Theta}{\pi}$$

Assuming that the threshold level of the cupula does not change from one type of experiment to another, this yields three ways of checking it. Thus:

$$\gamma_{min} = \alpha \tau = \frac{\alpha_{min}}{\omega} = \xi_{min} \frac{\pi}{\theta}$$

The three estimates are generally in agreement with an error of less than 25% and fall in the region of 1-2.5 degrees/sec.

Subjective Velocity: In the impulsive stop experiments in which the subject is brought to a sudden halt from a constant velocity rotation, the subjective feeling immediately following the halt is one of continued rotation in the original direction, gradually slowing down and finally decreasing to zero at the threshold time. Assuming that a certain subjective angular velocity corresponds to each position of deviation of the cupula, one could use estimates of subjective angular velocity to indicate the cupula position at any time. As mentioned previously, following an impulsive stop the cupula quickly rises to a level $\xi_{max} = \gamma \theta/\pi$, and then decreases exponentially toward zero with the time constant π/Δ. Estimates of subjective angular velocity determined from successive estimates of subjective angular position, were

established. A typical plot shown in Fig. 11 shows extremely good agreement with predictions. Note first of all that the extrapolated subjective velocity at time zero is almost exactly 40 degrees/sec, which was the true initial angular velocity of the subject. This lends credence to the relationship $\xi_{max} = \gamma \frac{\theta}{\pi}$ and, since θ/π has been estimated to be 0.1, leads to the conclusion that $\xi = 0.1\,\gamma$ for human subjects. Secondly, note that the decrease of subjective angular velocity with time follows the expected exponential decay, and plots as a straight line on the logarithmic plot of the above figure. The slope of this line (π/Δ = 10 sec) is in good agreement with the estimates obtained from the cupulograms.

Duration of Post-Rotation Nystagmus: The rhythmic motion of the eyes resulting from angular motion of the skull (vestibular nystagmus) may also be taken as an indication of cupula position. In general, the nystagmus consists of a slow phase in which the eyes move slowly in the direction opposite to the subjective rotation, and a quick phase in which the eyes jump rapidly back toward a central position before starting a new slow phase. The angular velocity of the slow phase of nystagmus is thought to be proportional to the deviation of the cupula. (Note that if the cupula position were always proportional to actual skull angular velocity as in the case of a true velocity meter, such an arrangement would permit nearly perfect stabilization of the eyes with respect to

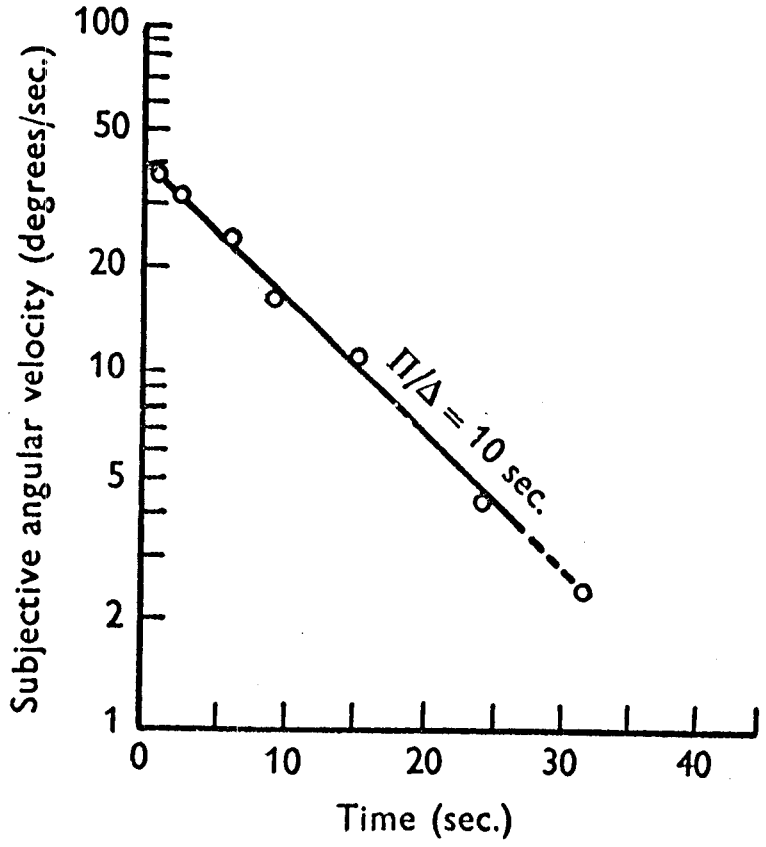


Fig. 11. Subjective angular velocity against time. The impulse administered was 40°/sec., as is the extrapolated subjective velocity. The slope gives $\Pi/\Delta = 10$ sec. (ref. 165)

the non-rotating environment.)

As an alternate method of determining cupulograms one may measure the duration of the post-rotation nystagmus. Two such cupulograms based on nystagmus are shown in Fig. 8. In general the threshold level of the nystagmus cupulogram is higher than the sensation level (5 - 15 degrees/sec as compared to 2 degrees/sec). This might be interpreted as indicating that the nystagmus threshold corresponds to a somewhat greater deviation of the cupula than does the sensation threshold. It is also to be noted that the nystagmus cupulogram is considerably steeper than the sensation cupulogram, and consequently indicates a higher estimate of π/Δ. Since the cupula may be expected to return to its steady state position in a unique fashion, presumably following the decay $e^{-\frac{\Delta}{\pi}t}$, one would expect its position to be reflected by the same rate of decrease of sensation in both subjective and nystagmus cupulograms. The difference in the slope of these two kinds of cupulograms presents a source of possible error in the theory.

Velocity of Nystagmus: The angular velocity of the eye during the slow phase of nystagmus may be measured following an impulsive stop to indicate the angular deviation of the cupula. Such a record is shown in Fig. 12. Just as in the case of the subjective estimate of angular velocity mentioned earlier, this plot supports the torsion pendulum theory in two details. The extrapolated initial angular velocity of nystagmus

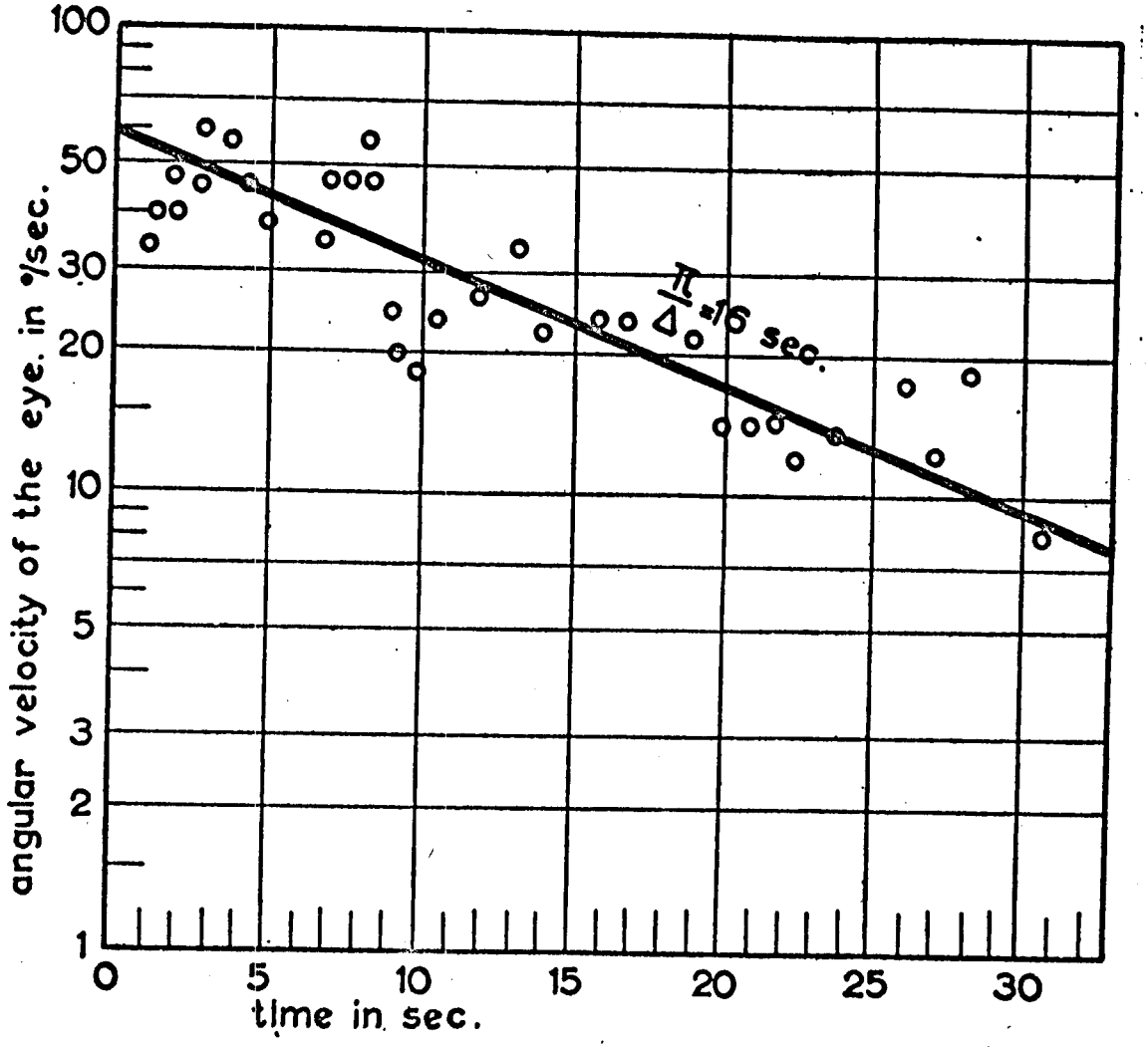


Fig. 12.

Angular velocity of the eye during the slow phase of the nystagmus (in darkness) as a function of time following an impulse of 60°/sec. The points are calculated from the recording. The extrapolation for $t=0$ gives a value of 59°/sec which appears to be almost equal to the original value. (ref. 73)

is very close to the true initial angular velocity of the subject. Furthermore, the decay of angular velocity of the eye is an exponential function of time, leading to an estimate of $\tau/\Delta = 16$ sec. This estimate of τ/Δ is consistent with the experimental evidence from the nystagmus cupulogram.

Phase Angle of Nystagmus Velocity: Just as the subjective response to sinusoidal accelerations was used by van Egmond et al. to estimate the system natural frequency, the phase angle of the velocity of the slow phase of nystagmus may be compared to the input angular velocity sinusoid to estimate the phase lag of the cupula at each test frequency. Hixson and Niven (92) present some preliminary results showing the steady state horizontal nystagmus produced by sinusoidal angular accelerations. An approximate curve of nystagmus phase lag with respect to angular acceleration may be deduced from the new data of Fig. 13. By arbitrarily assigning the nystagmus direction reversal at a point midway between fast phases in opposite directions, we calculate the following table:

Frequency (cps)	Phase Lag (degrees)
0.015	28
0.03	44.5
0.075	77.7
0.15	81.5
0.30	95.5

This data is plotted on Fig. 14 against a family of curves for the phase lag of simple second order system with different

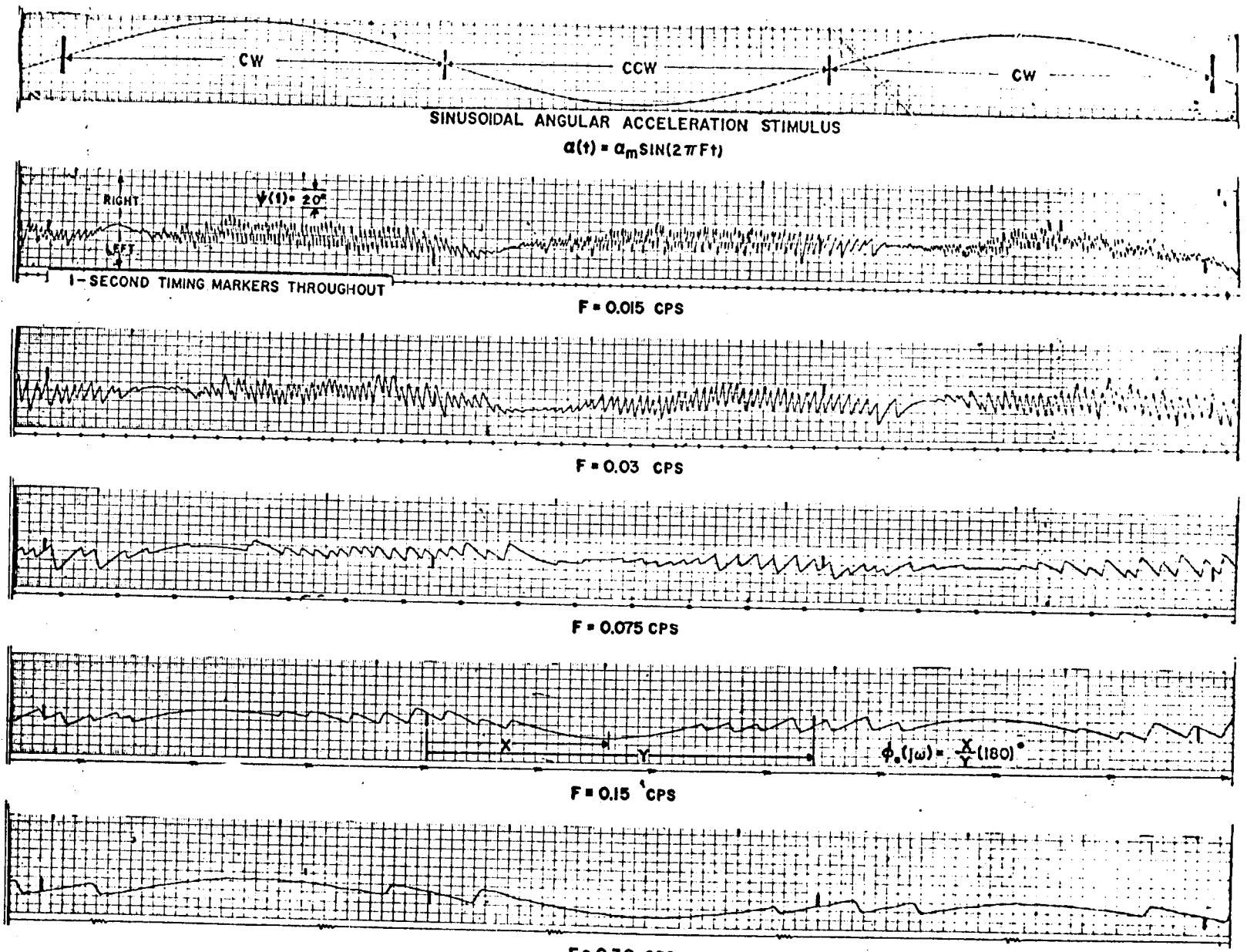


Fig. 13. STEADY STATE HORIZONTAL NYSTAGMUS RESPONSES AS PRODUCED BY SINUSOIDAL ANGULAR ACCELERATIONS OF VARIABLE FREQUENCY APPLIED ABOUT THE VERTICAL AXIS

(ref. 92)

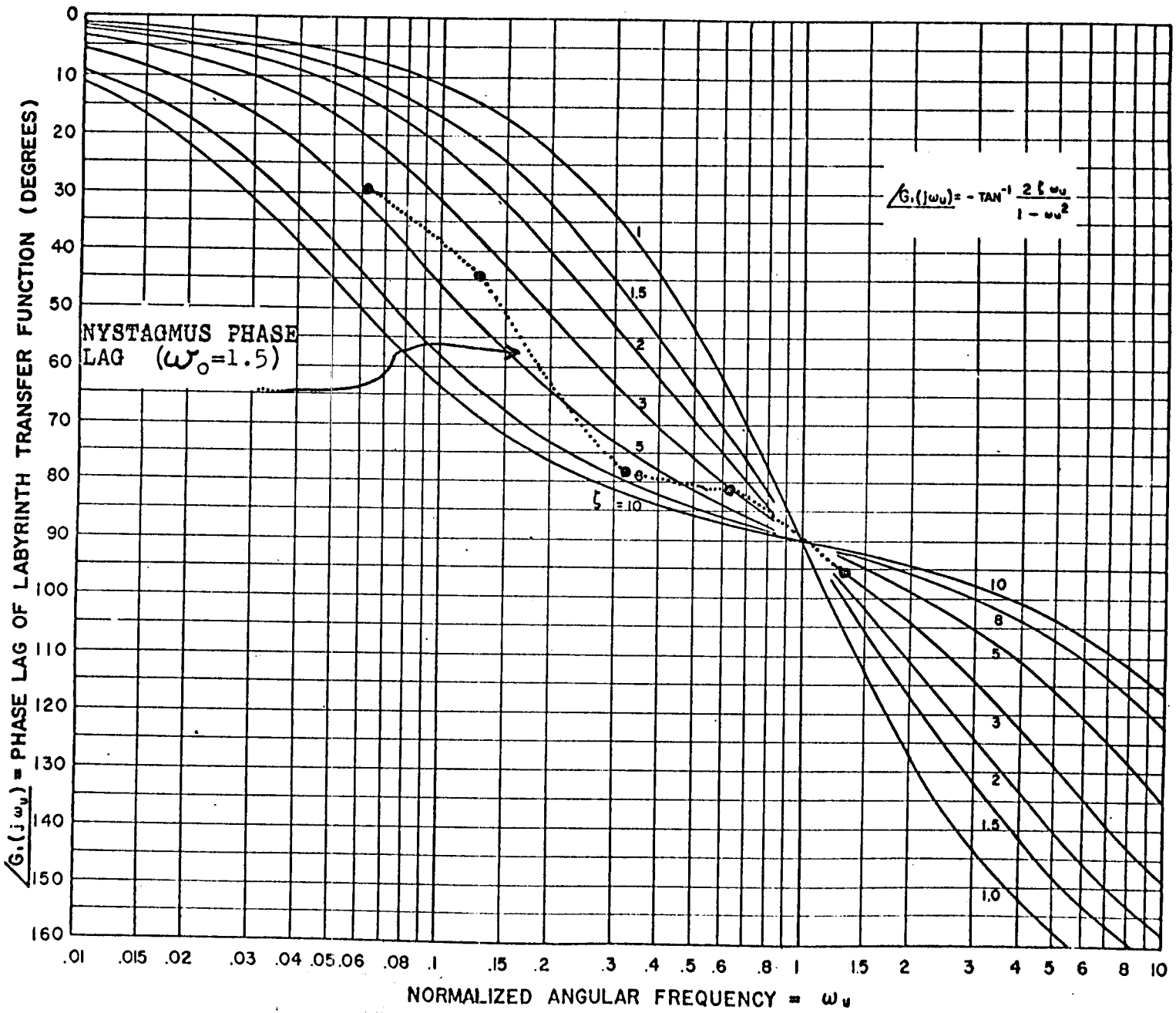

NYSTAGMUS PHASE LAG (ω_o=1.5)
$\angle G_1(j\omega_u) = -\tan^{-1}\frac{2\zeta\omega_u}{1-\omega_u^2}$
ζ =10
10
8
5
3
2
1.5
1.0
1
1.5
2
3
5
6
8
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
.01 .015 .02 .03 .04 .05 .06 .08 .1 .15 .2 .3 .4 .5 .6 .8 1 1.5 2 3 4 5 6 8 10
$\angle G_1(j\omega_u)$ = PHASE LAG OF LABYRINTH TRANSFER FUNCTION (DEGREES)
NORMALIZED ANGULAR FREQUENCY = ω_u

Fig. 14. (ref. 92)

damping coefficient. The nystagmus phase lag is forced to pass through 90 degrees at the resonance frequency by assuming,

$$\omega_0 = 1.5 \text{ rad/sec.}$$
$$(f_0 = 0.24 \text{ cps}).$$

Except for the data point at 0.075 cps the nystagmus phase lag versus frequency resembles that of a second order system with undamped natural frequency of 1.5 rad/sec. and damping constant of 3 - 4.

Assuming a damping constant of 4, the associated second order equation would be:

$$\ddot{\beta} + 12\dot{\beta} + 2.25 = 0$$

This compares to a reasonable degree with the equation parameter proposed by van Egmond et al., of

$$\ddot{\beta} + 10\dot{\beta} + 1 = 0$$

Detailed experiments of this type at a wide range of frequencies would be very helpful in detailed resolution of the amplitude and phase versus frequency characteristics of the cupula.

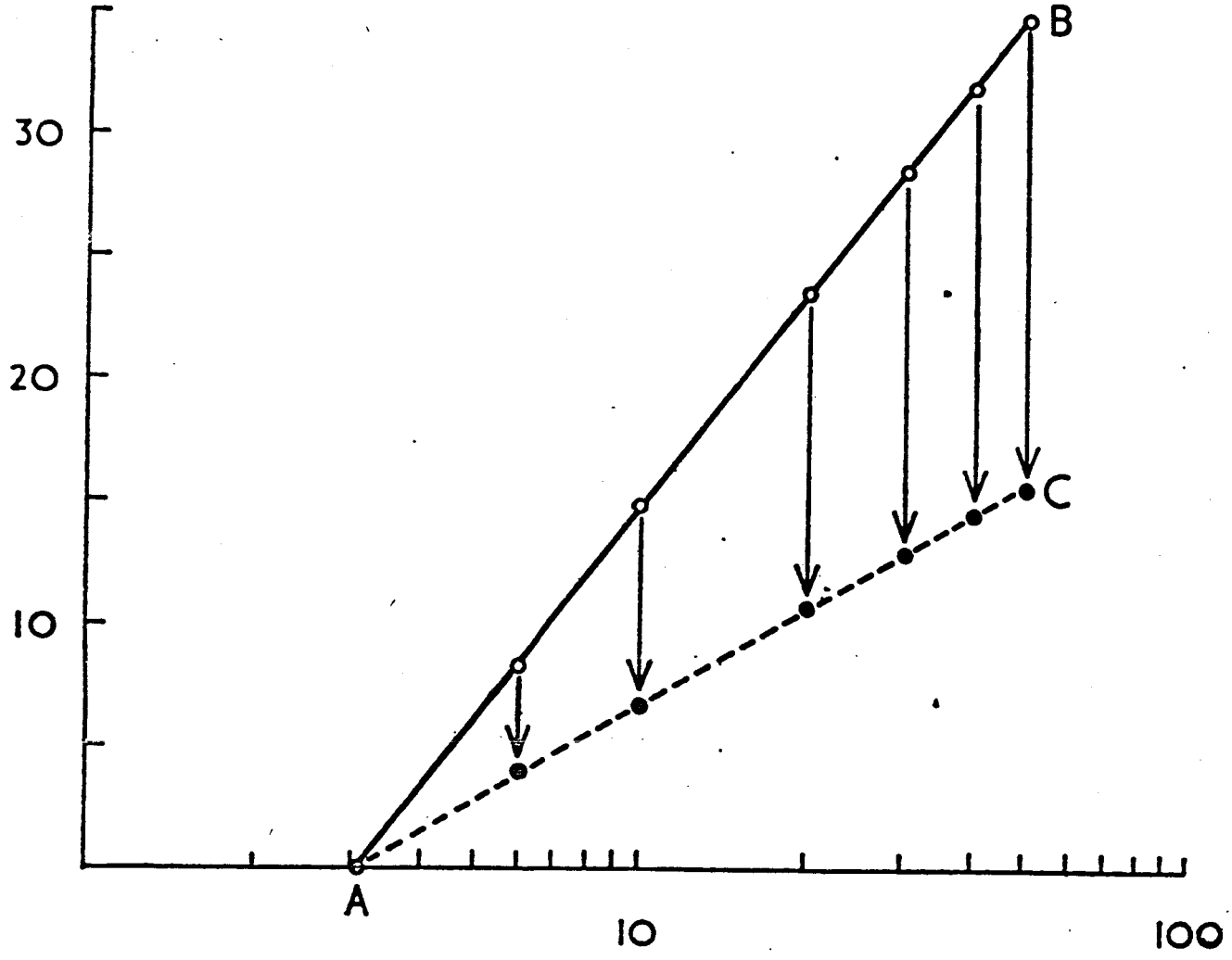
Habituation: The experimental data used in construction of the cupulograms described above were generally derived from successive tests on a given subject. The duration of post-rotation sensation following a certain level of impulse would be recorded, and the test then repeated for a higher impulse level until the entire range dictated by the cupulogram was covered. It has been pointed out that repeated determinations

of this cupulogram do not all have the same slope, thereby indicating a decreasing value of π/Δ. The apparent time constant of the cupulo-endolymph system would appear to decrease for repeated tests. In discussing this phenomenon, van Egmond et al. (165) were inclined to attribute it to a deformation of the cupula during the high impulse tests at the high end of the cupulogram. Such deformations, they reasoned, would increase the "leak" around the cupula in the ampulla, thereby leading to a system which would have a different time constant.

Cawthorne, Dix, Hallpike and Hood (19) attribute the change in slope of the cupulogram with repeated testing to a habituation phenomenon, probably occurring centrally. That is, although the cupula goes through the same physical deflection following each impulse, the central nervous system increases the effective threshold upon repeated stimulation. Fig. 15 shows how the successive determination of points on a single cupulogram could yield a curve of much lower slope than that which reflects the true time constant of the cupula, simply by habituation to successive stimuli. They argue that estimates of π/Δ taken from cupulograms must all be lower than the true value. (It will be recalled that the cupulogram parameters were generally 8 to 10 seconds whereas the value expected from theoretical considerations was approximately 27 seconds.)

Oculogyral Illusion: In an effort to overcome the habituation problem in determining π/Δ, Cawthorne et al. made use of the oculogyral illusion as an indicator of cupula position.

FIG. 15. DISTORTING EFFECT OF HABITUATION UPON SLOPE OF CUPULOGRAM



Abscissae: impulse (deg. sec.$^{-1}$)

Ordinates: duration (sec.)

AB: probable true form of cupulogram, without distortion by habituation

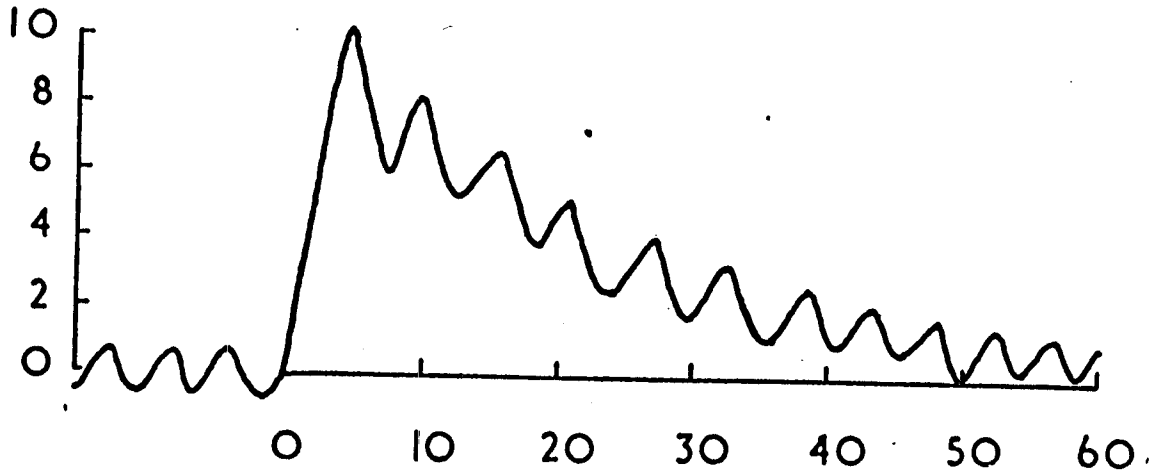
AC: cupulogram derived from responses to successive stimuli of increasing intensity

(ref 19)

The oculogyral illusion, as described by Graybiel and Hupp (69), is an illusion in which a visual reference point, rotating with the subject, will appear to move relative to the subject in the direction of rotation. It was attributed by Graybiel to movement of the image of the target across the retina during the slow phase of nystagmus. Thus toward the beginning of a slow rotation to the left, the semicircular canals indicate a velocity to the left and cause the eyes to move in nystagmus with the compensatory slow phase to the right, resulting in a relative movement of the target to the left with respect to the eyes during the slow phase. At present it is not clear whether the oculogyral illusion is, indeed, completely explained by the slow phase of nystagmus. Nevertheless, the velocity of the illusory movement may be taken as an indication of subjective velocity, and therefore an indication of cupula position. Cawthorne et al. used a psychophysical method to track the time course of oculogyral illusion following sudden cessation of rotation. The subject caused the target to assume a velocity which made it appear stationary to him. The magnitude of this cancelling velocity at all times could be taken as equal to the velocity of the oculogyral illusion.

A typical time course of the oculogyral illusion following a sudden halt is shown in Fig. 16. Note that it does show the rapid rise and slow exponential decay associated with the hypothetical cupula movement following such a stimulus. The rapid oscillations probably reflect the tracking technique of the psychophysical method, rather than any oscillatory cupula movement. Using curves of this type the decay constant of the cupula (T/Δ) could be determined on a single test, without introducing the

FIG. 16. TYPICAL RECORD OF SUBJECTIVE RESPONSE TO AN IMPULSIVE STIMULUS OF 40°sec.$^{-1}$



Abscissae: time (sec.)
Ordinates: light velocity (deg. sec.$^{-1}$)
(ref. 19)

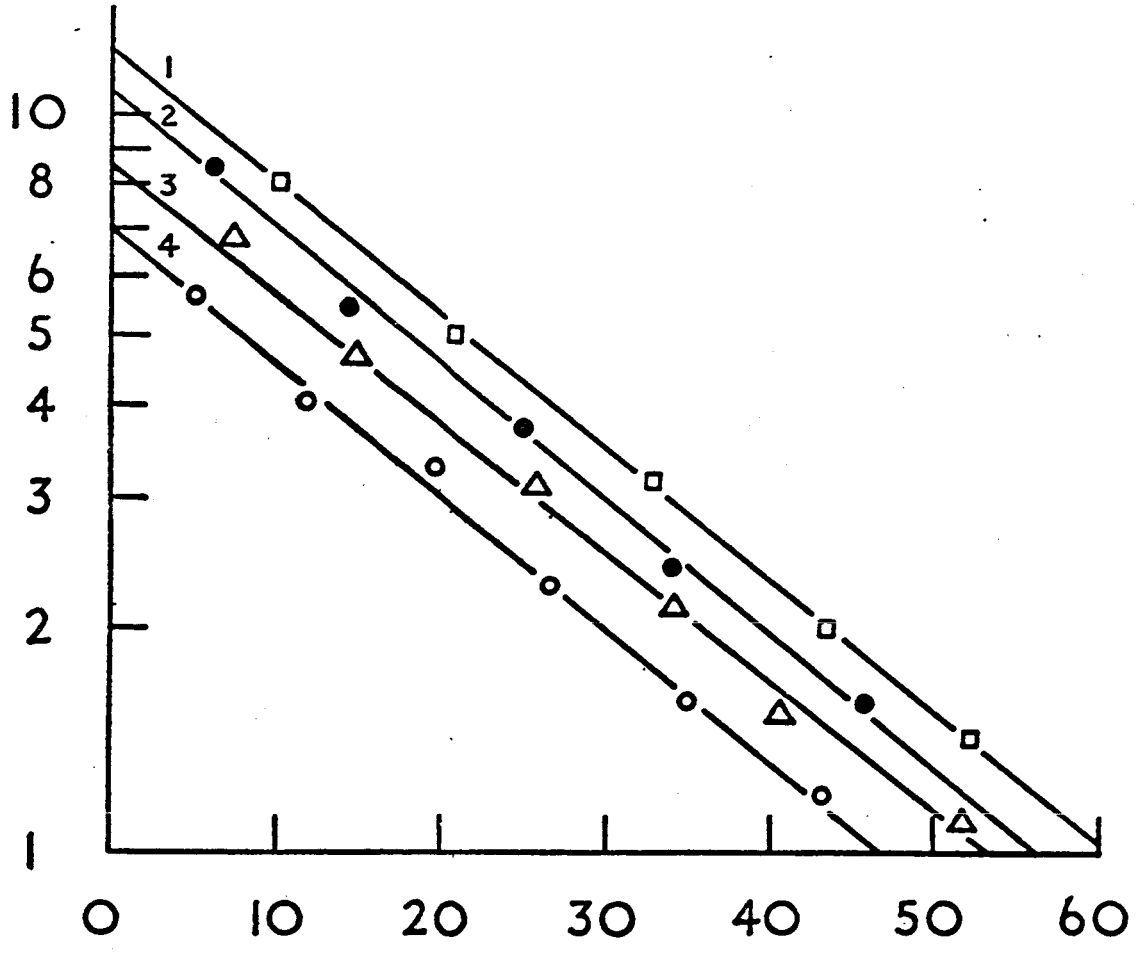
habituation difficulties of the normal cupulogram. A series of four such tests are shown in Fig. 17. The slope of these curves indicates a parameter value of

$$\tau/\Delta = 24.$$

This value is more than twice that obtained from sensation cupulograms, and quite close to the theoretical estimate. The effect of habituation is clearly seen, as the magnitude of the oculogyral illusion is shown to decrease with successive stimuli.

Caloric Stimulation: An entirely different means of stimulating semicircular canals involves the use of caloric stimulation. By pouring warm water into one ear, the temperature of the endolymph at a point closest to the water is raised, and convection currents are set up in the canal. These currents presumably act as a torque on the cupula and cause it to deflect just as would be the case following rotation. The direction of vestibular nystagmus observed following caloric stimulation agrees with such an interpretation. Tests using warm and cold water in the two ears show that the action of the semicircular canals is synergetic, and that the resultant vestibular rotation signal, as reflected by the direction of nystagmus, is the difference in cupula deflection of the two semicircular canals. The caloric tests are quite convenient and useful for clinical investigations of possible vestibular damage, but are not easily interpreted in terms of control theory descriptions of the system.

FIG. 17. RESPONSES TO FOUR IMPULSIVE STIMULI OF 40°sec.$^{-1}$ APPLIED IN SUCCESSION



Abscissae: time (sec.)
Ordinates: light velocity (deg. sec.$^{-1}$)
(ref. 19)

Threshold of Semicircular Canals to Rotation: It has been assumed that the threshold of sensation or nystagmus corresponds to a minimum deviation of the cupula (ξ°_{min}). As discussed earlier, Van Egmond et al., using impulse stimulations of sudden stopping of the subject from an initial angular velocity, found an average threshold level of $\gamma_{min} = 2.5$ degrees. Their torsion pendulum model indicates that this threshold impulse should be related to the threshold deviation of the cupula by the ratio of damping constant to moment of inertia. $\gamma_{min} = \frac{\pi}{\theta} \xi^{r}_{min}$ They show further that the Mulder product ($\alpha\tau$) necessary to reach sensation of rotation during constant acceleration, is approximately equal to γ_{min} as expected.

A slightly different test involves the minimum angular acceleration which can be sensed regardless of duration of that acceleration. The torsion pendulum model for a step of acceleration yields $\alpha_{min} = \frac{\Delta}{\theta} \xi^{r}_{min}$. In the case of constant acceleration notice that the spring constant of the cupula enters the equation, but the friction coefficient does not. Assuming that ξ^{r}_{min} is the same for both types of tests, we should find $\gamma_{min} = \frac{\pi}{\theta} \frac{\theta}{\Delta} \alpha_{min}$. Using the values $\frac{\theta}{\Delta}$ approximately equal to 1, as given by Van Egmond, the newer values $\frac{\pi}{\theta} = \frac{\pi}{\Delta} = 24$ found by Cawthorne et al., and $\gamma_{min} = 2.5$ °/sec., one would expect to find a threshold level of angular acceleration of α_{min} approximately equal to 0.1 deg/sec^2.

In the most sensitive tests reported to date, using the oculogyral illusion as an indicator, Graybiel, Kerr and Bartley (71) report a threshold for acceleration changes in both positive

and negative directions of 0.12 deg/sec^2. This is in very good agreement with the expected value from the torsion pendulum model and the impulse threshold data.

OTOLITHS

General:

The function of the otoliths in the vestibular system has long been recognized as providing sensitivity to gravity and linear acceleration. The mass of the otolith, which is considerably more dense than that of the surrounding fluid, is acted upon by inertial forces and displaced in the direction of the specific force acting on the body, thereby shifting its position over the macula and indicating the direction of the specific force. This function has repeatedly been shown on birds and sea animals. It is not clear, however, whether the magnitude of the net specific force is also signaled by the otoliths. The otoliths may be able to indicate the direction of the vertical, for example, but not to measure the force of gravity. If this were the case they would not be true vector sensors, but could be considered to be transducers which yield a unit vector directed along the true specific force vector.

By the very nature of the otolith-macula-endolymph configuration its dynamic behavior should resemble that of a second order system. The inertial mass corresponds to that of the otolith, the spring constant to the supporting hairs from the macula, and the damping to the viscous force between the otolith and endolymph.

One would expect considerably higher natural frequency and lower damping constant than for the larger semicircular canals. Almost no fundamental research has been undertaken, however, to describe the function of the otolith or experimentally determine the values of the parameters which affect its operation. Probably the major reason for this situation stems from the difficulty of performing experiments in which the otoliths are stimulated and the semicircular canals are not.

Static Behavior - Perception of the Vertical:

One of the principal tasks of the otolith portion of the vestibular system is the indication of the direction of vertical for postural control. In a long series of experiments Asch and Witkin (5, 6, 177, 178) investigated the factors which bear on human perception of the upright. Of particular interest to this study was their series of experiments on the ability of subjects to perceive the direction of vertical without any visual cues, while they were tilted to various orientations (177). They found that judgments of the vertical were very accurate when the head and body are upright, with mean errors of the order of 2 degrees. When the head or body was tilted from the erect position, however, the ability to judge the vertical on the basis of non-visual cues was found to be severely hampered. The errors increase with the amount of body tilt, reaching a maximum when the body is in a horizontal position. (Other investigations show that errors are still greater for inverted subjects.) The mean range for judgments

of the vertical when the subject was tilted 28 degrees from the true vertical was approximately 10 degrees.

Adaptation Effects in Perception of the Vertical:

Do we " forget " the true vertical when we have been exposed to a new orientation in space? Adaptation effects in perception of the vertical in the absence of visual cues were investigated by Passey and Guedry (136). Their subjects were placed in a Link trainer and at various initial attitudes, and asked to return themselves to "straight and level". They found that the final orientations were consistently skewed toward the direction of the initial attitude. The amount of adaptation is of the order of 60% of the initial angular displacement. Passey and Guedry state, "Following exposure to tilt for a period of sixty seconds, readjustments to the gravitational vertical are significantly less accurate than under immediate readjustment, and the number of errors in the direction of initial inclination is significantly greater under a condition of exposure to inclination, giving evidence of adaptation."

It was mentioned, in the discussion of the anatomy and physiology of the otolith, that nerve endings were discovered which respond only to changes in otolith position on the macula. They might function in a manner to permit the central nervous system a degree of adaptation to any steady state direction of specific force. If this were the case control theory description of the otolith would include a term of the form: $\frac{1}{TS+1}$, where T represents the characteristic time of the adaptation.

Tracking the Direction of the Apparent Vertical in the Absence of Visual Cues:

The direction of the apparent vertical, or vector sum of gravity and linear acceleration, may be changed by rotating the subject in a 1"g" field, or by keeping the subject upright and subjecting him to linear acceleration. Clark and Graybiel (30) used an approximation to the latter method to determine the subjective perception of vertical in the absence of visual cues when the direction of the apparent vertical is varied. They placed a subject on a rotating centrifuge. The slowly varying radial acceleration from the centrifuge, added to the normal 1"g" field, produced a change in the direction of apparent vertical up to 36 degrees from the true vertical. The subjects attempted to maintain a line at the subjective horizontal during the experiments. A typical tracking result is shown in Fig. 18. The data shows the subjective estimate of orientation to be quite accurate for angles of less than 10 degrees between body and the apparent vertical, whereas for angles of greater than 30 degrees the subjects tended to overestimate the angle of tilt. When the same tests were repeated with a long period of constant radial acceleration, no significant differences were found in the ability of the subject to estimate the horizontal after the rotation has been decreased to zero. These results are in agreement with those of Witkin and Asch, showing greater errors in perception of the vertical for larger angles of

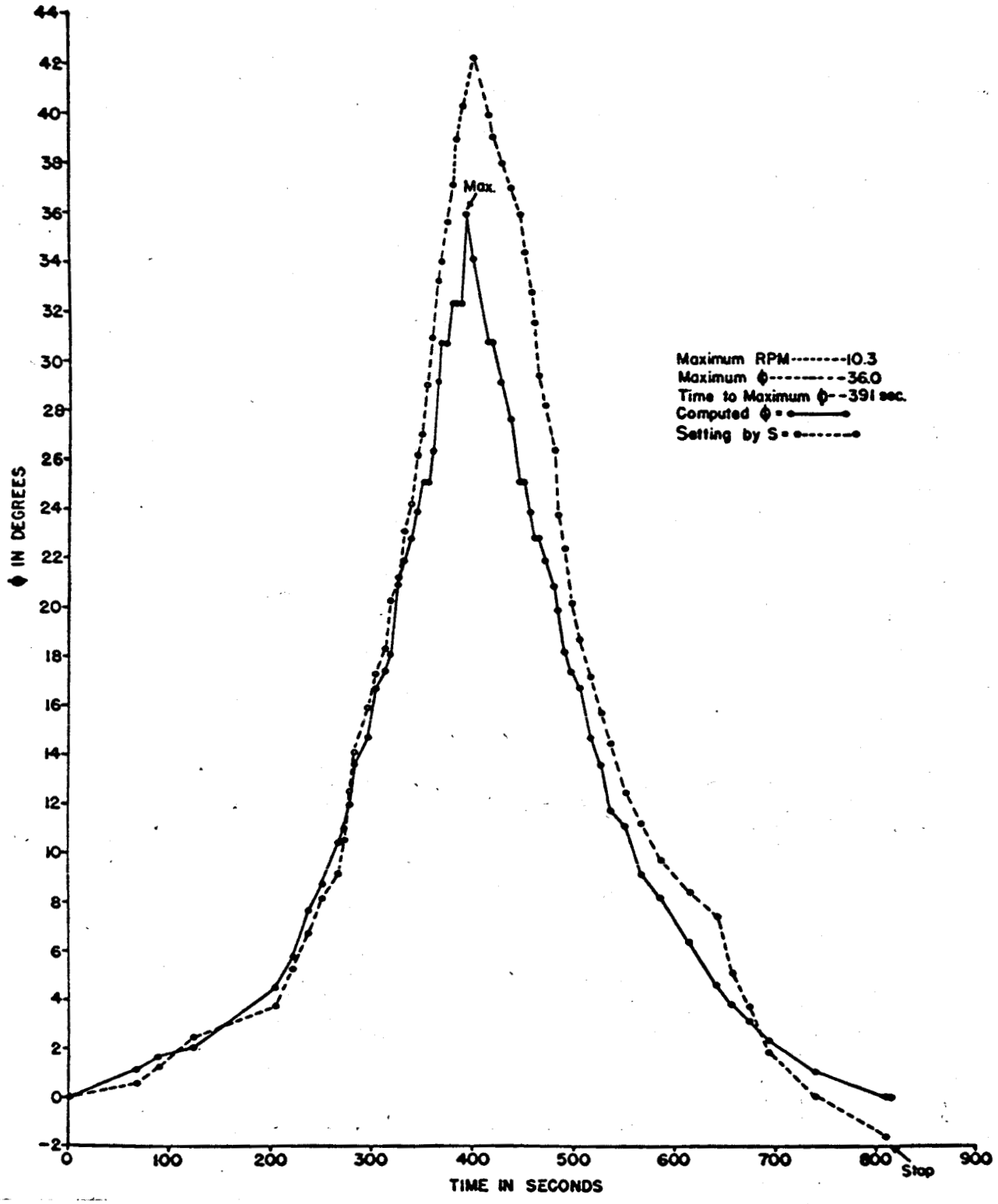


FIG. 18. THE COMPUTED VALUE OF ϕ AND THE SETTING OF THE LINE BY SUBJECT S DURING A SINGLE TRIAL IN PART I (ref. 30)

tilt, but do not bear out the findings of Passey and Guedry showing significant adaptation when exposed to a non-vertical orientation. The explanation for this difference probably lies in the time taken to vary the tilt of the subject. Clark and Graybiel conjecture that the adaptation effect in perception of orientation only comes into play if the orientation is changed rapidly but not if the direction of the resultant force with respect to the body is changed slowly.

"Step Response" Stimulation of the Otoliths:

Using the same test procedure as mentioned above, Graybiel and Brown (65) investigated the delay in reorientation of the perceived vertical when the direction of the apparent vertical was changing rapidly. This was accomplished as before placing the subject on a centrifuge and quickly accelerating it up to constant velocity, thereby suddenly changing the direction of specific force. The result of the subject's estimation of the horizontal without visual cues are shown in Fig. 19. This experiment might be interpreted as a possible step response to stimulation of the otoliths, in which the direction of specific force is changed quickly. Interpreted in this light, we would find an extraordinarily long time constant (of the order of 25 seconds) following the increase in α. A puzzling result is the lack of symmetry in returning toward $\alpha = 0$ as the centrifuge stops and the apparent horizontal comes into agreement with the true horizontal. Rather than attribute these assymmetric step responses to some nonlinearity in the

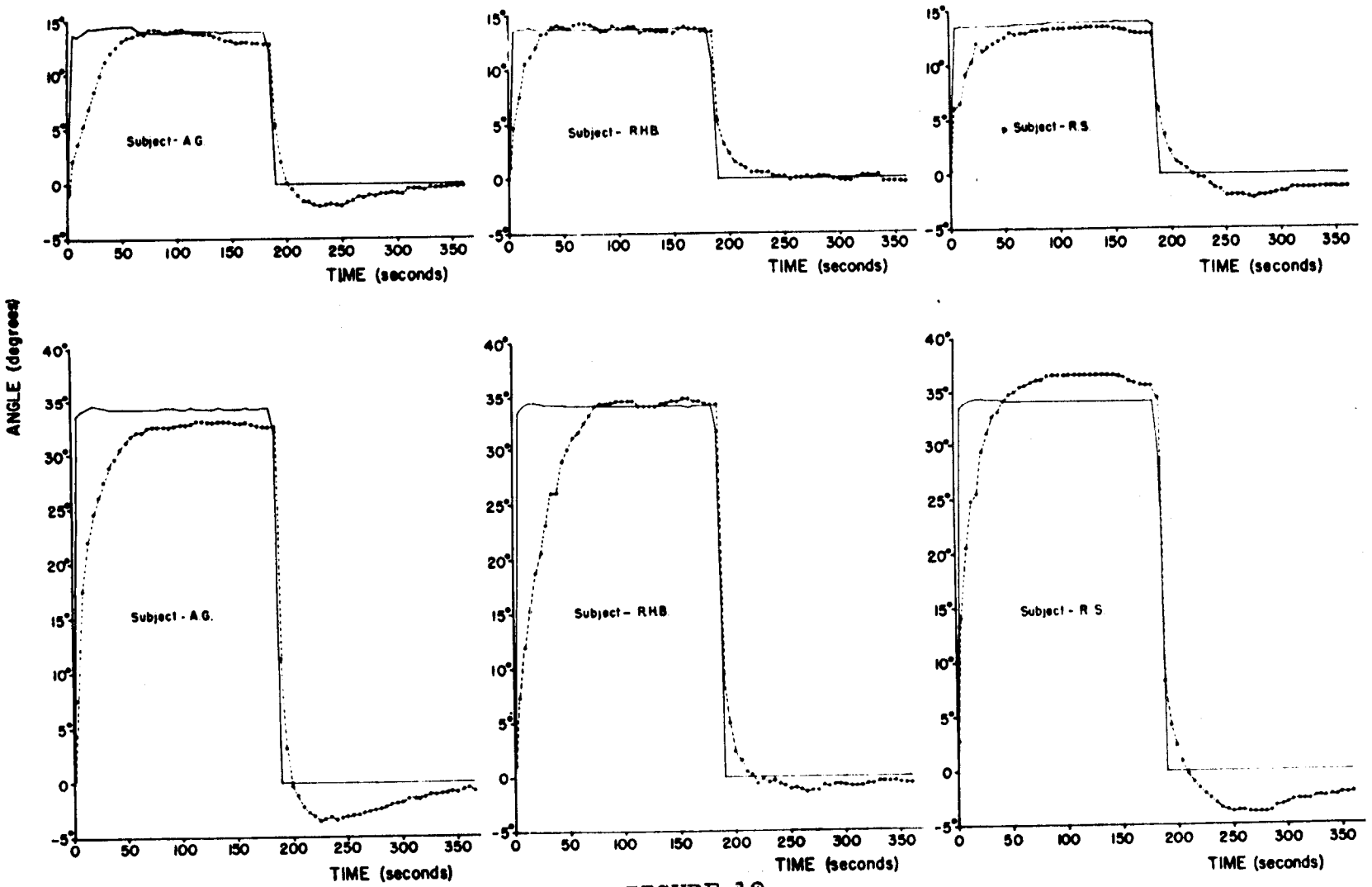


FIGURE 19.

SHIFT IN THE DIRECTION OF RESULTANT FORCE AND OF VISUAL ORIENTATION FOLLOWING ONSET OF CENTRIFUGAL FORCE
The solid curve indicates the deviation of resultant force from gravitational vertical. The broken curve represents the change in the subject's estimate of the horizontal. Each point is the average of 10 measurements on separate trials for each of the three subjects.

otolith, and attribute characteristic time of 25 to 30 seconds to the otoliths, we prefer to interprete this experiment as indicating the effect of subject "set" and cross coupling from stimulation of the semicircular canals. Since the subjects knew the experimental conditions and were aware of their rotation in the centrifuge by stimulation of the semicircular canals, they could not be expected to immediately assume that the new direction of apparent vertical was the "true vertical". The long time constant must therefore be interpreted as a combination of vestibular and tactile input information as well as the complex "reorientation" process going on in the central nervous system.

Flotation Experiments:

In all of the experiments described above, the subjects received tactile information through the pressure on their skin. Experiments in well-padded seats show greater variability in estimation of the direction of vertical than when nonambiguous tactile cues were present, thereby indicating that the tactile cues were by no means insignificant. Tactile cues can be eliminated by flotation of the subject in a pool of water, where the pressure over the entire body is approximately constant. Since the internal organs are not floated they will continue to respond to the specific force, but it may be assumed that the primary internal specific force sensor is the vestibular system. Under conditions of flotation in the absence of visual cues

subjects are as likely to swim down toward the bottom of the pool as not, when directed to swim toward the surface. The inability to correctly judge the vertical when in any orientation except those quite close to the erect position is clearly shown by such experiments.

Sinusoidal Stimulation and Threshold of Perception:

Using a simple swing apparatus to produce sinusoidal linear accelerations, Walsh (170) investigated the threshold level of subjective sensation of linear motion. By using several stimulus frequencies he could determine whether such thresholds were dependent upon linear displacement, velocity, acceleration or jerk. As expected threshold is acceleration dependent and is of the approximate value 10 cm/sec^2 or about 0.01 "g". These thresholds were all determined for the subject lying down on a stretcher, and do not indicate what the threshold level would be in the erect position. Of further interest in this test are the phase relationships between subjective perception of movement and the actual movement as a function of frequency. Subjects reported the direction in which they thought they were moving. At 1 cps oscillations, the subjective estimate was generally correct and in phase with the actual movement. At 1/3 and 1/9 cps, however, the subjective estimate was approximately 90 degrees ahead of the actual movement and the subject would indicate that he was moving in a certain direction when the swing had just come to the end point prior to moving in that direction.

If the assumption is made that the subject interprets the output of the otolith as indicating the acceleration of his motion, this bit of data may be used in estimating the frequency response of the system. His subjective response is in phase with the maximum acceleration at 1/3 and 1/9 cps. At 1 cps, however, he is in phase with the maximum velocity and thereby indicates a 90 degree phase lag of the system. If only first order characteristics are considered, the break frequency of the system would fall between 1/3 and 1 cps. Assuming a break frequency of 0.5 cps (ω_o = 3.1 rad/sec) a time constant of approximately 0.3 seconds could be assigned to the otolith system. Such a time constant would be much more in keeping with the expected behavior of the system from a mechanical point of view.

V. CONTROL MODELS FOR THE VESTIBULAR SYSTEM.

On the basis of the experimental data discussed in the previous section control models for the functioning of the semicircular canals and otoliths may be constructed. The block diagrams of Fig. 20 reflect those characteristics which are known to be present in the vestibular mechanism. Considering first the block diagram representation of the semicircular canals, the input is assumed to be angular acceleration of the skull with respect to inertial space ($\dot{\omega}_{I_A}$). The matrix transformation [A] projects the inertial angular acceleration vector along the input axes of the three semicircular canals. The semicircular canal dynamics relate the output (ζ) of the cupula to the input angular acceleration in terms of a highly damped second order model. Approximate values for the break frequencies are:

$$\Delta/\pi = 0.04 - 0.1 \text{ rad/sec}$$

$$\pi/\Theta = 10 - 25 \text{ rad/sec}$$

The threshold level of cupula displacement for sensation is about

$$\zeta_{min} = 0.1 - 0.2 \text{ degrees}$$

under conditions of no adaptation to rotation.

The conversion from cupula displacement to pulse frequency introduces a saturation for large negative accelerations or

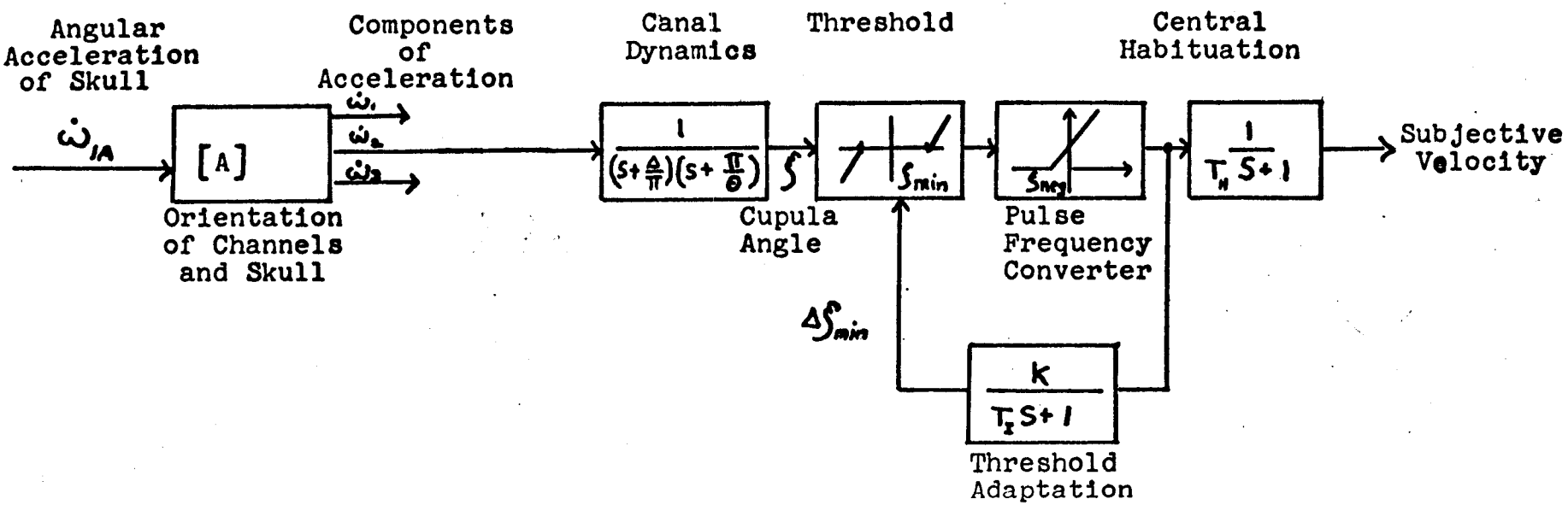


Fig. 20(a) Semicircular Canal Block Diagram

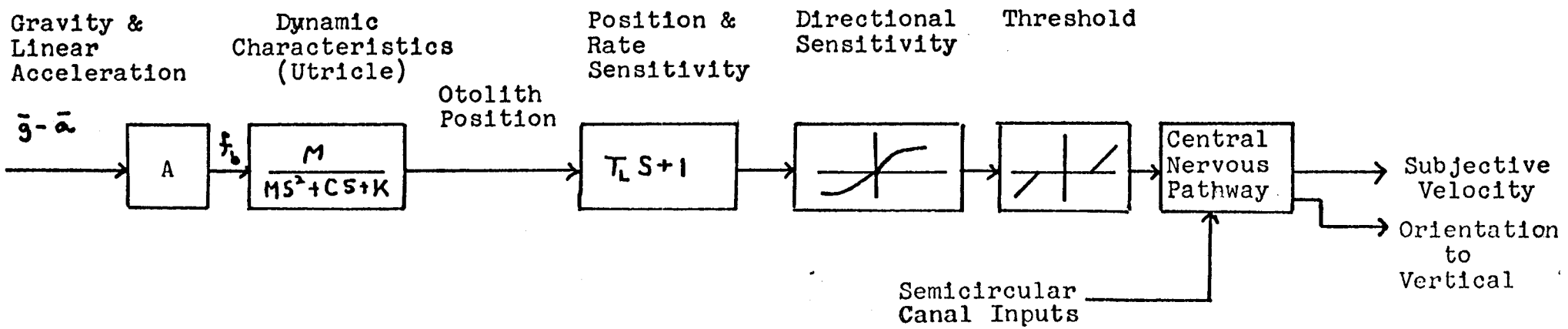


Fig. 20(b) Otoliths Block Diagram

negative cupula displacements for each semicircular canal; however, the value of S°_{neg} has not been determined. The block marked "central habituation" represents the long time adaptation to successive stimulation of the semicircular canals, as shown by cupulogram tests. T_H is a long time constant, probably on the order of hours or days.

The threshold adaptation block is assumed to increase the minimum threshold for sensitivity to sensation of rotation and occurrence of nystagmus following a history of angular acceleration. The output of the system is assumed to be subjective sensation of angular velocity.

Over most of the spectrum of head movements encountered in normal activity the semicircular canal system does indeed act to give indications which represent velocity rather than acceleration. Using slightly different values of the parameters in the second order model for the semicircular canals, Mayne (120) calculated the frequency response shown in Fig. 21. (Note that over the region 10 to 400 cycles/minute the output of the system in terms of cupula displacement is indeed proportional to the input velocity.) The difference of opinion often voiced on this matter stems from a misunderstanding of the functioning of a second order system. A mass-spring-dashpot system is not an accelerometer or a velocity meter or a vibrometer per se, but only acts as a sensor of one of these elements in a certain frequency range. For a heavily damped second order system such

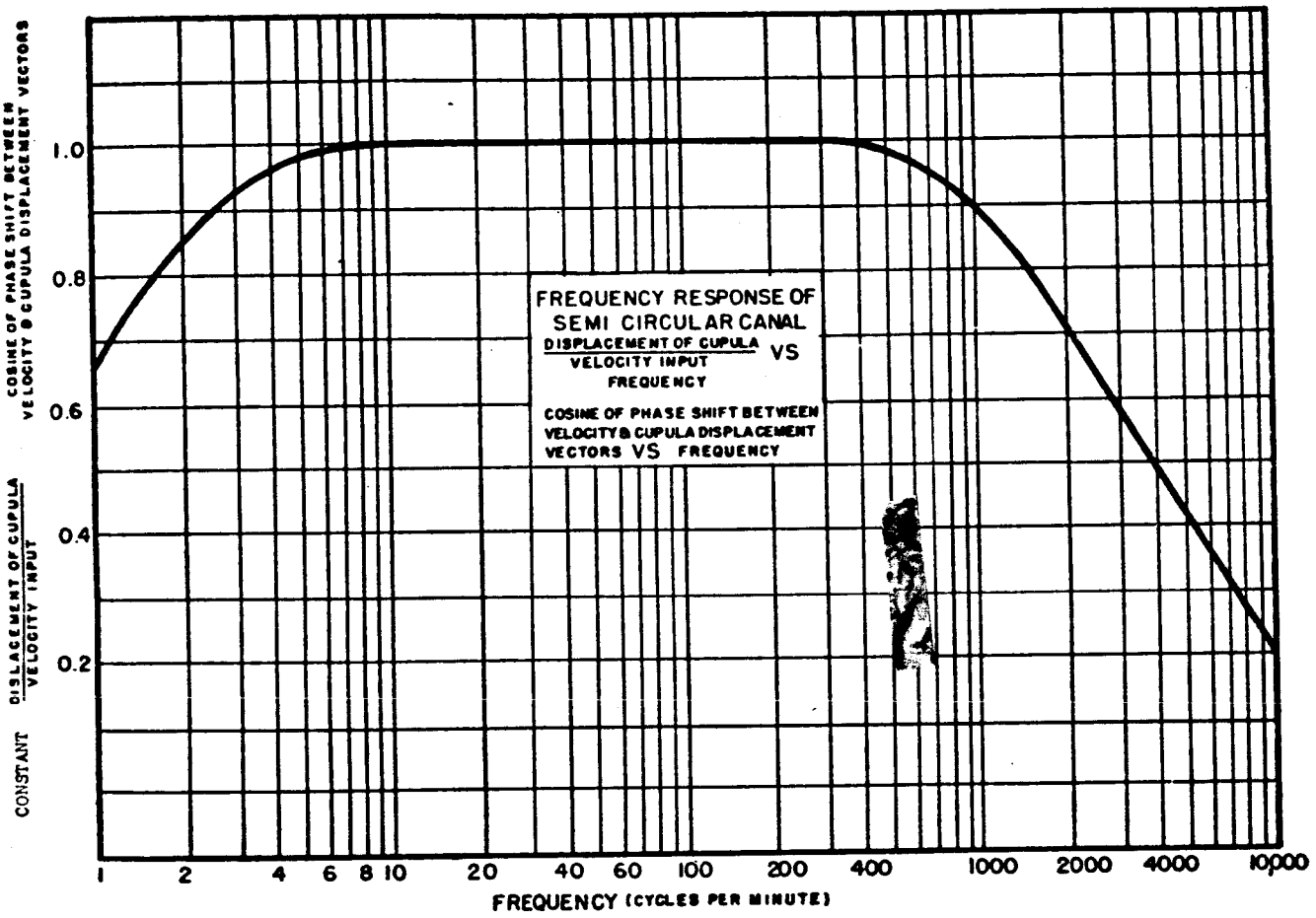


Fig. 21. Frequency Response of Semicircular Canal (Ref 120)

as the semicircular canals, the large middle range over which its phase lag is approximately 90 degrees makes it particularly useful as a velocity meter for these frequencies.

The principal remaining control tasks in the investigation of the semicircular canal involve the magnitude of the threshold, the time course of central and threshold habituation, and the effectiveness of the semicircular canal system incorporated as an active error sensor in a closed loop system.

The otolith block diagram shown in Fig. 20b reflects what little is known about the otoliths to date. The specific force input of gravity minus acceleration is resolved by the orientation of the otolith with respect to the skull and the skull with respect to inertial space to yield a set of specific force outputs f_b acting on the otoliths. The dynamic characteristics of the otolith-macula system in the utricle are represented by the mass M, spring constant K, and damping C of the mechanical arrangement. No data is available on the magnitude of these parameters, however. The presence of cells whose output is proportional to the change in position of the otolith rather than in its position is represented by the box "position & rate sensitivity". Once again, no detailed investigation of T_L, the lead time constant, has been conducted.

It is known that the otoliths are primarily sensitive to changes in orientation away from the erect position, and are not particularly sensitive to changes in orientation when the subject is tilted at a large angle. This phenomenon is

represented by the saturation curve in the block labeled "directional sensitivity". The otoliths also have a threshold to linear acceleration of about 0.01 "g".

Quite obviously the interpretation of otolith outputs in the central nervous system is effected by the presence of other outputs from the semicircular canals, and the subjective linear velocity and orientation with respect to the vertical must be considered as resulting from both systems. Experiments have yet to be carried out in which the otolith control characteristics are carefully investigated in the absence of semicircular canal stimulation.

BIBLIOGRAPHY

1. Adams, J.A., L.R. Creamer, Anticipatory Timing of Continuous and Discrete Responses, J. Exper. Psych., 63:84-90, 1962.
2. Adrian, E.D., Discharges from Vestibular Receptors in the Cat, J. Physiol., London, 101:389-407, 1943.
3. Agin, L.J., S.G. Marcum, F.J. Daugherty, M.B. Ferrell, and F.N. Trager, Airsickness and Related Psychosomatic Complaints, Air Surgeon's Bulletin, 2:235, 1945.
4. Armstrong, C.R., Space Physiology, J. British Interplanetary Society, 12:172-175, 1953.
5. Asch, S.E., H.A. Witkin, Studies in Space Orientation: I. Perception of the Upright with Displaced Visual Fields, J. Exper. Psych., 38:325-337, 1948.
6. Asch, S.E., H.A. Witkin, Studies in Space Orientation: II. Perception of the Upright with Displaced Visual Fields and with Body Tilted, J. Exper. Psych., 38:455-477, 1948.
7. Aschan, G., Response to Rotary Stimuli in Fighter Pilots, Acta Oto-laryngologica, Supp. 116, 1954.
8. Bahrick, H.P., P.M. Fitts, G.E. Briggs, Learning Curves-Facts or Artifacts, Psych. Bull. 54:256-268, 1957.
9. Bahrick, H.P., P.M. Fitts, R. Schneider, Reproduction of Simple Movements as a Function of Factors Influencing Proprioceptive Feedback, J. Exper. Psych., 49:445-454, 1955.
10. Barlow, J.S., Inertial Navigation as a Basis for Animal Navigation, Neurophysiology Laboratory of the Neurology Service, Mass. General Hospital, Boston, Mass.
11. Birren, J.E., in Human Factors in Underseas Warfare, Chapter 18, National Research Council, Washington, D.C., 1949.
12. Bridges, C.C., Bitterman, M.E., The Measurement of Autokinetic Movement, Amer. J. Psych., 67:525-529, 1954.
13. Brodal, A., Fiber Connections of the Vestibular Nuclei, in Neural Mechanisms of the Auditory and Vestibular Systems, Charles C. Thomas, Springfield, Ill., 224-246, 1960.
14. Brodal, A., O. Pompeiano, F. Walberg, The Vestibular Nuclei and their Connections, Anatomy and Functional Correlations, Charles C. Thomas, Springfield, Ill., 1962.
15. Brown, J.L., M. Lechner, Acceleration and Human Performance, J. Aviation Med., 27:32-49, 1956.
16. Campbell, E.H., The Effectiveness of Dramamine in Relieving the Vestibular Reactions Following the Labyrinthine Fenestration Operation. Laryngoscope, 59:1261-1272, 1949.
17. Carpenter, M.B., Experimental Anatomical-Physiological Studies of the Vestibular Nerve and Cerebellar Connections, in Neural Mechanisms of the Auditory and Vestibular Systems. Ed. G.L. Rasmussen and W.F. Windle, Charles C. Thomas, Springfield, Ill., pp. 297-323.

18. Carmichael, E.A., M.R. Dix and C.S. Hallpike, Pathology, Symptomatology and Diagnosis of Organic Affections of the Eighth Nerve System. Brit. Med. Bull., 12:146-152, 1956.
19. Cawthorne, T., et al., The Investigation of Vestibular Function. Brit. Med. Bull., 12:131-142, 1956.
20. Cawthorne, T.E., G. Fitzgerald and S.C. Hallpike, Studies in Human Vestibular Function. II. Observations on the Directional Preponderance of Caloric Nystagmus ("Nystagmusbereitschaft") Resulting from Unilateral Labyrinthectomy. Brain, 65:138-160, 1942.
21. Chase, R.A., S. Harvey, S. Standfast, I. Rapin and S. Sutton, Studies on Sensory Feedback. I: Effect of Delayed Auditory Feedback on Speech and Keytapping. Q.J. Exp. Psychol., 13:141-167, 1961.
22. Chinn, H., and P.K. Smith, Motion Sickness, Pharmacol. Rev., 7:33-82, 1955.
23. Clark, B., and A. Graybiel, Antecedent Visual Frame of Reference as a Contributing Factor in the Perception of the Oculogravic Illusion. Bur. of Med. & Surg., Project MR005.13-6001, Subtask 1, Report No. 56.
24. Clark, B., and A. Graybiel, The Breakoff Phenomenon. J. Aviation Med., 28:121-126, 1957.
25. Clark, B., and A. Graybiel, Contributing Factors in the Perception of the Oculogravic Illusion. Am. J. Psychol., 76:18-27, 1963.
26. Clark, G., and A. Graybiel, Human Performance during Adaptation to Stress in the Pensacola Slow Rotation Room. J. Aerospace Med., No. 32, February, 1961.
27. Clark, B., and A. Graybiel, The Lag Effect Associated with Stimulation of the Semicircular Canals as Indicated by the Oculogyral Illusion. U.S. Naval Sch. of Aviation Medicine, Project Report No. NM 001 059.01.25, Nov, 1950.
28. Clark, B., and A. Graybiel, Perception of the Postural Vertical as a Function of Practice in Normal Persons and Subjects with Labyrinthine Defects. Bur. Med. & Surg., Project MR005.13-6001, Subtask 1, Report No. 63, 1961.
29. Clark, B., and A. Graybiel, Vertigo as a Cause of Pilot Error in Jet Aircraft. J. Aviation Med., 28:469-478, 1957.
30. Clark, B., and A. Graybiel, Visual Perception of the Horizontal following Exposure to Radial Acceleration on a Centrifuge. J. Comp.& Physiol. Psychol., 44:525-534, 1951.
31. Clark, B., A. Graybiel, and K. MacCorquodale, The Illusory Perception of Movement Caused by Angular Acceleration and by Centrifugal Force during Flight. II. Visually Perceived Motion and Displacement of a Fixed Target during Turns. J. Exp. Psychol., 38:298-309, 1948.
32. Clark, B., and M.A. Nicholson, Aviator's Vertigo: A Cause of Pilot Error in Naval Aviation Students. J. Aviation Med., 25:171-179, 1954.
33. Clegg, W.C. and N.M. Dunfield, Non-Visual Perception of the Postural Vertical: II. Lateral Plane. Canad. J. Psychol., 8:80-86, 1954.

34. Collins, W.E., Further Studies of the Effects of Mental Set upon Vestibular Nystagmus. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 443, 1960.
35. Collins, W.E., C.H. Crampton and J.B. Posner, The Effect of Mental Set upon Vestibular Nystagmus and the Electroencephalogram, US Army Med. Res. Lab., Fort Knox, Ky., Report No. 439, 1960.
36. Collins, W.E. and F.E. Guedry, Jr., Arousal Effects and Nystagmus during Prolonged Constant Angular Acceleration. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 500, 1961.
37. Collins, W.E., F.E. Guedry, Jr., and J.B. Posner, Control of Caloric Nystagmus by Manipulating Arousal and Visual Fixation Distance. US Army Med. Res. Lab., Fort Knox., Ky., Report No. 485, 1961.
38. Cramer, R.L., Response of Mammalian Gravity Receptors to Sustained Tilt. J. Aero. Med., 33:663-666, 1962.
39. Crampton, G.H. and W.J. Schwam, Effects of the Arousal Reaction on Nystagmus Habituation in Cat. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 434, 1960.
40. Crossman, E.R.F.W., The Information-Capacity of the Human Motor-System in Pursuit Tracking. Q.J. Exp. Psychol., 12:1-16, 1960.

41. Dearnaley, E.J., et al., Nature and Duration of After-Sensations following the Cessation of Turning in a Chipmunk Aircraft. J. Aero. Med., October, 1962.
42. DeWit, G., Seasickness (Motion Sickness), A Labyrinthological Study. Acta Oto-Laryng., Supp. 108:1-56, 1953.
43. Dix, M.R. and C.S. Hallpike, Lesions of the Cerebral Hemispheres and their Effects upon Optokinetic and Caloric Nystagmus. J. Physiol., 114:55, 1951.
44. Dodge, R. Thresholds of Rotation. J. Exp. Psychol., 6:107-137, 1923.
45. Dohlman, G., Histochemical Studies of Vestibular Mechanisms., Neural Mechanisms of the Auditor and Vestibular Systems. Ed. by G.L. Rasmussen and W.F. Windle, Charles C. Thomas, Springfield, Ill., pp. 258-275, 1960.
46. Dohlman, G., J. Farkashidy, and F. Saloona, Centrifugal Nerve Fibers to the Sensory Epithelium of the Vestibular Labyrinth. J. Laryng. Otol., 72:984-991, 1958.

47. Engstrom, H., On the Double Innervation of the Sensory Epithelia of the Inner Ear. Acta Oto-laryng., Stockholm, 49:109-118, 1958.

48. Fitts, P.M., The Information Capacity of the Human Motor System in Controlling the Amplitude of Movement. J.Exp. Psychol., 47:381-391, 1954.

49. Fitzgerald, G. and C.S. Hallpike, Studies in Human Vestibular Functions: I. Observations on Directional Preponderance ("Nystagmusbereitschaft") of Caloric Nystagmus Resulting from Cerebral Lesions. Brain, 65:115-137, 1942.
50. Fleishman, E.A., The Influence of Fixed Versus Free Head Position on the Perception of Body Position. Human Resources Res. Center, Lackland Air Force Base, Tex., Res. Bull. 53-37, Oct, 1953.
51. Fleishman, E.A., The Perception of Body Position --Effect of Speed, Magnitude, and Direction of Displacement on Accuracy of Adjustment to an Upright Position. Human Resources Res. Center, Lackland Air Force Base, Tex., Res. Bull. 53-1, Jan, 1953.
52. Fleishman, E.A., Perception of Body Position in the Absence of Visual Cues. J. Exp. Psychol., 24:176-187, 1953.
53. Furey, J.A. and R.N. Kraus, A Clinical Classification of Vertigo. Aeromed. Reviews, Rev. 7-61, Apr, 1962.

54. Gacek, R.R., Efferent Component of the Vestibular Nerve., Neural Mechanisms of the Auditory and Vestibular Systems. Ed. by G.L. Rasmussen and W.F. Windle, Charles C. Thomas, Springfield, Ill., pp. 276-284, 1960.
55. Gauer, O.H. and G.D. Zuedeman, Gravitational Stress in Aerospace Medicine. Little Brown and Co., 1961.
56. Gerathewohl, S.J. and H.D. Stallings, Experiments during Weightlessness: A Study of the Oculo-Agravic Illusion. J. Av. Med., 29:504-516, 1958.
57. Gerathewohl, S.J. and H.D. Stallings, The Labyrinthine postural reflex (righting reflex) in the cat during weightlessness. J. Av. Med. 28:345, 1957.
58. Gerebtzoff, M.A., Des Effets de la Stimulation Labyrinthique sur l'activite Electrique de l'encore Cerebrale., C.R. Soc. Biol., Paris, 131:807-813, 1939.
59. Gerebtzoff, M.A., Recherches sur la Projection Corticale de Labyrinthe. I. Des Effects de la Stimulation Labyrinthique sur l'activite Electrique de l'ecorce Cerebrale., Arch. Int. Physiol. 50:59-99, 1940.
60. Gerebtzoff, M.A., Recherches sur la Projection Corticale de Labyrinthe. I. Etude Anatomo-Experimentale de la Voie Vestibulo-Cerebrale. J. Belge Neurol. Psychiat., No. 8: 417-432, 1940.
61. Gernandt, B., Midbrain Activity in Response to Vestibular Stimulation. Acta Physiol. Scand., 21:73-81, 1950.
62. Gernandt, B.E. and S. Gilman, Generation of Labyrinthine Impulses, Descending Vestibular Pathways, and Modulation of Vestibular Activity by Proprioceptive, Cerebellar, and Reticular Influences., Neural Mechanisms of the Auditory and Vestibular Systems. Ed. by G.L. Rasmussen and W.F. Windle, Charles C. Thomas, Springfield, Ill., pp. 324-348, 1960.

63. Gooddy, W. and M. Reinhold, Some Aspects of Human Orientation in Space. (i) Sensation and Movement. Brain 75:472-509, 1952.
64. Gooddy, W. and M. Reinhold, Some Aspects of Human Orientation in Space. (ii) The Dynamic Nature of Nervous Activity. (a) "Motion Sense" (b) Sense of Direction. Brain, 76:337-363, 1953.
65. Graybiel, A. and R.H. Brown, The Delay in Visual Reorientation Following Exposure to a Change in Direction of Resultant Force on a Human Centrifuge. J. Gen. Psychol. 45:143, 1951.
66. Graybiel, A. and B. Clark, Perception of the Horizontal or Vertical with Head Upright, On the Side, and Inverted under Static Conditions, and during Exposure to Centripetal Force. J. Aero. Med., 33:147-155, 1962.
67. Graybiel, A., B. Clark and J.J. Zarriello, Observations on Human Subjects Living in a "Slow Rotation Room" for Periods of Two Days. AMA Arch. Neurol. 3, July 1960.
68. Graybiel, A., F.E. Guedry, W. Johnson and R. Kennedy, Adaptation to Bizarre Stimulation of the Semicircular Canals as Indicated by the Oculogyral Illusion. J. Aero. Med., 32: 321-327, 1961.
69. Graybiel, A. and D. Hupp, The Oculogyral Illusion: A Form of Apparent Motion Which May Be Observed following Stimulation of the Semicircular Canals. J. Avia. Med., 17:3, 1946
70. Graybiel, A. and W.H. Johnson, A Comparison of the Symptomatology Experienced by Healthy Persons and Subjects with Loss of Labyrinthine Function When Exposed to Unusual Patterns of Centripetal Force in a Counter-Rotating Room. Ann. Otol, Rhinol. and Laryngol., 72:357, 1963.
71. Graybiel, A., W.A. Kerr and S.H. Bartley, Stimulus Thresholds of the Semicircular Canals as a Function of Angular Acceleration. Am. J. Psychol. 61:21-36, 1948.
72. Graybiel, A., J.I. Niven, T.E. Walsh, The Differentiation between Symptoms Referable to the Otolith Organs and Semicircular Canals in Patients with Nonsuppurative Labyrinthitis. The Laryngoscope, 62:924-933, 1952.
73. Groen, J.J., O. Lowenstein and A.J.M. Vendrik, The Mechanical Analysis of the Responses from the End Organs of the Horizontal Semicircular Canal in the Isolated Elasmobranch Labyrinth. J. Physiol., London, 117:329-346, 1952.
74. Guedry, F.E., Jr. and N. Beberman, Apparent Adaptation Effects in Vestibular Reactions. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 293, Aug, 1957.
75. Guedry, F.E., Jr. and S.J. Ceran, Derivation of 'Subjective Velocity' from Angular Displacement Estimates Made during Prolonged Angular Accelerations: Adaptation Effects. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 376, 1959.
76. Guedry, F.E., Jr., W.E. Collins, and P.L. Sheffey, Perceptual and Oculomotor Reactions to Interacting Visual and Vestibular Stimulation. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 463, Mar, 1961.
77. Guedry, F.E., Jr., R.L. Cramer and W.P. Koella, Experiments on the Rate of Development and Rate of Recovery of Apparent

Adaptation Effects in the Vestibular System, US Army Med. Res. Lab., Fort Knox, Ky., Report No. 336, June, 1958.
78. Guedry, F.E., Jr. and A. Graybiel, The Appearance of Compensatory Nystagmus in Human Subjects as a Conditioned Response during Adaptation to a Continuously Rotating Environment. Bur. of Med. & Surg., Project MR005.13-6001, Subtask 1, Report No. 61.
79. Guedry, F.E., Jr. and A. Graybiel, Compensatory Nystagmus Conditioned during Adaptation to Living in a Rotating Room. J. App. Physiol. 17: May 1962.
80. Guedry, F.E., Jr. and H. Kalter, Description of Human Rotation Device. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 242, May, 1956.
81. Guedry, F.E., Jr., and L.S. Lauver, The Oculomotor and Subjective Aspect of the Vestibular Reaction during Prolonged Constant Angular Acceleration, US Army Med. Res. Lab., Fort Knox, Ky., Report No. 438, Sept 1960.
82. Guedry, F.E., Jr., and E.K. Montague, Relationship between Magnitudes of Vestibular Reactions and Effective Coriolis Couples in the Semicircular Canal System. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 456, Dec. 1960.
83. Guedry, F.E., Jr., L.J. Peacock, and R.L. Cramer, Nystagmic Eye Movements during Interacting Vestibular Stimuli. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 275, March, 1957.

84. Hammer, L.R., Perception of the Visual Vertical under Reduced Gravity. Technical Documentary Report No. MRL-TRL-62-55, Wright Patterson Air Force Base, Ohio, May 1962.
85. Hartinger, H., Motion and Perception of Space. USAF Sch. Av. Med., Special Report, 1951.
86. Hartman, B.O., The Effect of Target Frequency on Compensatory Tracking. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 272, April 1957.
87. Hawkes, G.R., R.W. Bailey, and J.S. Warm, Method and Modality in Judgments of Brief Stimulus Duration. US Army Med. Res. Lab., Fort Knox, Ky., Report No. 442, Sept 1960.
88. Hemingway, A., Results of 500 Swing Tests for Investigating Motion Sickness. AAF Sch. Av. Med., Randolph AFB, Res. Project 31, Report No. 2, Nov 1942.
89. Henry, F.M., Dynamic Kinesthetic Perception and Adjustment. Res. Quart. Am. Assoc. of Health & Physical Ed., 24:176-187, 1953.
90. Henry, J.P., et al., Effects of Weightlessness in Ballistic and Orbital Flight. J. Aero. Med., Sept., 1962.
91. Hick, W.E., The Discontinuous Functioning of the Human Operator in Pursuit Tasks. Q.J. Exp. Psychol., 1:36-52, 1948.
92. Hixson, W.C. and J.I. Niven, Application of the System Transfer Function Concept to a Mathematical Description of the Labyrinth: I. Steady-State Nystagmus Response to

Semicircular Canal Stimulation by Angular Acceleration. Bureau of Med. & Surg., Project MR005.13-6001, Subtask 1, Report No. 57, 1961.

93. Howland, D. and M.E. Noble, The Effect of Physical Constants of a Control on Tracking Performance. J. Exp. Psychol., 46:353-360, 1953.

94. Johnson, W.H., Head Movement Measurements in Relation to Spatial Disorientation and Vestibular Stimulation. J. Av. Med., 27:148-152, 1956.

95. Johnson, W.H., The Importance of Head Movements in the Production of Motion Sickness. J. Def. Res. Bd., Canada, Library of Congress, Tech. Info. Div. No. U22185, Apr. 1952.

96. Johnson, W.H., and J.W. Mayne, Stimulus Required to Produce Motion Sickness: Restriction of Head Movements as a Preventive of Airsickness - Field Studies on Airborne Troops. J. Av. Med., 24:400-411, 1953.

97. Johnson, W.H., J. Meek and A. Graybiel, Effects of Labyrinthectomy on Canal Sickness in Squirrel Monkey. Ann. Otol., Rhinol., & Laryngol., 71:289, 1962

98. Johnson, W.H., J. Meek and A. Graybiel, The Effects of Unilateral and Bilateral Labyrinthectomy on Canal Sickness in the Squirrel Monkey. Bureau of Med. & Surg., Project MR005.13-6001, Subtask 1, Report No. 65.

99. Johnson, W.H. and B. Smith, Functions of the Utricular Macula. A Preliminary Report. Can. J. Biochem. Physiol., 37:605-606, 1959.

100. Kennedy, R.S. and A. Graybiel, Symptomatology during Prolonged Exposure in a Constantly Rotating Environment at a Velocity of One Revolution per Minute. Bureau of Med. & Surg., Project MR005.13-6001, Subtask 1, Report No. 62.

101. Kennedy, R.S. and A. Graybiel, Symptomatology during Prolonged Exposure in a Constantly Rotating Environment at a Velocity of One Revolution per Minute. J. Aero. Med., 33:817-825, 1962.

102. Kraus, R.N., Disorientation in Flight: An Evaluation of the Etiological Factors. Aero. Med., 30:664-673, 1959.

103. Lansburg, M.P., Some Considerations and Investigations in the Field of Labyrinthine Functioning. IV. Influences of Vestibular-stimulation upon Electro-encephalogram, Electro-cardiogram and Respiration. Aeromedica Acta, (Soesterberg, Netherlands), 3:241-246, 1954.

104. Levy, C.K. and H. Quastler, Acute Responses of the Vestibular Apparatus to X-irradiation. Radiation Research, 16:189-200, 1962.

105. Loftus, J.P., ed., Symposium on Motion Sickness with Special Reference to Weightlessness. Technical Documentary Report No. AMRL-TDR-63-25, June 1963.
106. Lowenback, H. and W.H. Gantt, Conditional Vestibular Reactions. J. Neuro. Physiol, J. 4348, 1940.
107. Lowenstein, O., The Equilibrium Function of the Vertebrate Labyrinth. Biol. Rev., 11:113-145, 1936.
108. Lowenstein, O. and A. Sand, The Activity of the Horizontal Semicircular Canal of the Dogfish, Scyllium canicula. J. Exp. Biol., 13:416-428, 1936.
109. Lowry, R.H. and W.H. Johnson, 'Pseudo Motion Sickness' Due to Sudden Negative 'G': Its Relation to 'Airsickness'. J. Av. Med., April, 1954.

110. MacCorquodale, K., Effects of Angular Acceleration and Centrifugal Force on Nonvisual Space Orientation During Flight. J. Av. Med., 19:146-157, 1948.
111. Magnus, R., Animal Posture (The Croonian Lecture). Proc. R. Soc. (B.), 98:339-353, 1925.
112. Magnus, R., Some Results of Studies on the Physiology of Posture. Lancet, pp. 531-536 and 585-588, 1926.
113. Mann, C.W., Final Technical Report. Joint Project Report No. 43, USN Sch. Av. Med., Pensacola, Fla., 1956.
114. Mann, C.W., Visual Factors in the Perception of Verticality. J. Exp. Psychol., 44:460-464, 1952.
115. Mann, C.W., Which Way is Up?. Research Reviews, ONR, Dept. Navy. Oct. 1951.
116. Mann, C.W., N.H. Berthelot-Berry and H.J. Dauterive, Jr., The Perception of the Vertical: I. Visual and Non-Labyrinthine Cues. J. Exp. Psychol., 39:700-707, 1949.
117. Mann, C.W., C.J. Canella and A. Graybiel, An Examination of the Technique of Cupulometry. Joint Project Report No. 42, US Naval Sch. Av. Med., Pensacola, Fla., May 1956.
118. Mann, C.W. and G.E. Passey, The Perception of the Vertical: V. Adjustment to the Postural Vertical as a Function of Postural Tilt and Duration of Exposure. J. Exp. Psychol., 41:108-113, 1951.
119. Mann, C.W. and J.T. Ray, The Perception of the Vertical: XIV. The Effect of the Rate of Movement on the Judgment of the Vertical. Naval Sch. Av. Med. and Tulane U., Joint Project Report No. 40, 1956.
120. Mayne, R., Some Engineering Aspects of the Mechanism of Body Control. Electrical Engineering, 70:207-212, 1951.
121. McCabe, B.F., Vestibular Suppression in Figure Skaters. Trans. Amer. Acad. Opth. and Otol., 64:1960.
122. McFarland, R.A., Human Factors in Air Transportation, McGraw-Hill Book Co., N.Y., 1953.
123. McNally, W.J., The Otoliths and the Part They Play in Man. Laryngoscope, 54:304-323, 1944.
124. McNally, W.J. and E.A. Stuart, Physiology of the Labyrinth Reviewed in Relation to Seasickness and Other Forms of Motion Sickness. War Medicine, 2:683-771, 1942.
125. Mickle, W.A. and H.W. Ades, Rostral Projection Pathway of the Vestibular System. Amer. J. Physiol., 176:243-252, 1954.

126. Miller, E.F. and A. Graybiel, A Comparison of Ocular Counterrolling Movements between Normal Persons and Deaf Subjects with Bilateral Labyrinthine Defects. Joint Report, Bureau of Med. & Surg., Project MR005.13-6001, Subtask 1, Report No. 68, 1962.
127. Miller, E.F. and A. Graybiel, Role of the Otolith Organs in the Perception of Horizontality. Joint Report, Bureau Med. & Surg., Project MR005.13-6001, Subtask 1, Report No. 80, 1963.
128. Moore, E.W. and R.L. Cramer, Perception of Postural Verticality. USAF Sch. Av. Med., TDR-62-72, June 1962.
129. Morant, R.B., The Visual Perception of the Median Plane as Influenced by Labyrinthian Stimulation. J. Psychol., 47:25-35, 1959.
130. Morrell, F., Electrophysiological Contributions to the Neural Basis of Learning. Physiol. Rev. 443-494, 1961.

131. Niven, J.L. and W.C. Hixson, Frequency Response of the Human Semicircular Canals: Steady-State Ocular Nystagmus Response to High-Level Sinusoidal Angular Rotations. Bureau Med. & Surg., Project MR005.13-6001, Subtask 1, Report No. 58.
132. North, J.D., Z.A. Lomnicki and S.K. Zaremba, The Design and Interpretation of Human Control Experiments. Ergonomics, 1:314-327, 1957-58.
133. Nuttall, J.B., The Problem of Spatial Disorientation. J. A.M.A., 166:431-438, 1958.
134. Nuttall, J.B. and W.G. Sanford, Spatial Disorientation in Operational Flying. USAF Norton AFB, San Bernardino, Calif., Report No. M-27-56, May 1956.

135. Passey, G.E., The Perception of the Vertical. IV. Adjustment to the Vertical with Normal and Tilted Visual Frames of Reference. J. Exp. Psychol., 40:738-745, 1950.
136. Passey, G.E. and F.E. Guedry, Jr., The Perception of the Vertical: II. Adaption Effects in Four Planes. J. Exp. Psychol. 39:700-707, 1949.
137. Petroff, A.E., An Experimental Investigation of the Origin of Efferent Fiber Projections to the Vestibular Neuro-epithelium. (Abstract) Anat. Rec., 121:352-353, 1955.
138. Pfaltz, C.R., Die Normale Calorische Labyrinthreaktion., Arch. Ohren- usw. Heilk. u. Z. Hals- usw. Heilk., Bd. 172: 131-174, 1957.
139. Pfaltz, C.R. and R. Gulick, Die Pathologische Calorische Labyrinthreaktion. Arch. Ohren- usw. Heilk. u. Z. Hals- usw. Heilk., Bd. 179:525-544, 1962.
140. Pfaltz, C.R. and R. R. Pfaltz, Zur Prufung der Wirksamkeit Vestibular Angreifender Pharmaka. HNO, 11:165-169, 1963.
141. Pigg, L.O. and Kama, W.N., Visual Acuity in Relation to

Body Orientation. Wright-Patterson AFB, Technical Documentary Report MRL TDR-62-74, 1962.
142. Poulton, E.C., On the Stimulus and Response in Pursuit Tracking. J. Exp. Psychol. 53:189-194, 1957.

143. Quix, F.H., Epreuves Vestibulaires. L'Oto-Rhino-Laryng. Internat. 6:484, 1922.

144. Rasmussen, G.L. and R. Gacek, Concerning the Question of an Efferent Fiber Component of the Vestibular Nerve of the Cat. (Abstract) Anat. Rec., 130:361-362, 1958.
145. Razran, G., The Observable Unconscious and the Inferable Conscious in Current Soviet Psychophysiology: Interoceptive Conditioning, Semantic Conditioning and the Orienting Reflex. Psych. Rev., 68:1961.
146. Richter, Hs.R., and C.-R. Pfaltz, Recherches nystagmographiques sur la Reaction Vestibulaire Galvanique. Confinia Neurologica, 18:370-377, 1958.
147. Roman, J.A., B.H. Warren and A. Graybiel, Observation of the Elevator Illusion during Subgravity Preceded by Negative Accelerations. Joint Report, Bureau Med. & Surg., Project MR005.13-6001, Subtask 1, Report No. 83, 1963.
148. Roman, J.A., B.H. Warren and A. Graybiel, The Sensitivity to Stimulation of the Semicircular Canals during Weightlessness. Joint Report, Bureau Med. & Surg., Project MR 005.13-6001, Subtask 1, Report No. 84, 1963.

149. Scher, S.H. Pilot's Loss of Orientation in Inverted Spins. National Advisory Committee for Aeronautics, Tech. Note 3531, Langley Aeron. Lab., Langley Field, Va., Oct 1955.
150. Schock, G.J.D., Apparent Motion of a Fixed Luminous Target during Sub-gravity Trajectories. Technical Report 58-3, AF Missile Development Center, Holloman AFB, N.M., 1958.
151. Schwab, R.S., The Nonlabyrinthine Causes of Motion Sickness. Internat. Record Med., 167:631-637, 1954.
152. Simons, D.G., Sub-gravity and Weightlessness in Gravitational Stress in Aerospace Medicine. Ed. by Gauer and Zuidema, G.D. Little Brown and Co., Boston, 189-201, 1961.
153. Smith, P.E., on "Physiological Responses" in Simulation Council Newsletter, ed. by J. McLeod, p.119, Aug 1962, in Instruments and Control Systems.
154. Solley, C.M., Reduction of Error with Practice in Perception of the Postural Vertical. J. Exp. Psychol., 52:329-333, 1956.
155. Spiegel, E.A., Effect of Labyrinthine Reflexes on the Vegetative Nervous System. Arch. Oto-Laryng., 44:61, 1946.
156. Spiegel, E.A., G.C. Henry and H.T. Wycis, Changes of Cerebral Circulation Induced by Labyrinthine Stimulation. Am. J. Physiol., 142:589-593, 1944.
157. Spiegel, E.A., M.J. Oppenheimer, G.C. Henry and H.T. Wycis, Experimental Production of Motion Sickness. War. Med., 5:283, 1944.

158. Spiegel, E.A. and J. Sommer, Vestibular Mechanisms. Med. Physics., Ed. by O. Glasser. The Year Book Publishers Inc., Chicago, 1638-1653 (Vol. I) and 399-401 (Vol. 2) 1950.
159. Steele, J.E., Motion Sickness and Spatial Perception: A Theoretical Study. ASD Technical Report 61-530, 1961.
160. Steinhausen, W., Uber den Nachweis der Bewegung der Cupula in der Intakten Bogengangsampulle des Labyrinthes dei der Naturlichen Rotatorischen und Calorischen Reizung. Pflugers Arch. ges. Physiol., 228:322-328, 1931

161. Tyler, D.B. and P. Bard, Motion Sickness. Physiol. Rev., 29:311-369, 1949.

162. Useller, J.W. and J.S. Algranti, Pilot Control of Space Vehicle Tumbling. Nat. Specialists Meeting on Guidance of Aerospace Vehicles, N.Y., 1960, pp. 109-113.
163. Useller, J.W. and J.S. Algranti, Pilot Reaction to High-Speed Rotation. IAF Meeting, Stockholm, 1960.
164. U.S. Dept. H.E. & W., Public Health Service, National Library of Medicine, Ref. Div., Bibliography of Space Medicine. Publication No. 617, 1958.

165. Van Egmond, A.A.J., J.J. Groen and L.B.W. Jongkees, The Mechanics of the Semicircular Canal. J. Physiol. 110:1-17, 1949.
166. Van Sickle, M.D., Modern Airmanship, 2nd Ed. New York: D. Van Nostrand & Co., Inc., 1961.
167. Vinacke, W.E., Aviator's Vertigo. J.Av. Med. 19:158-170, 1948.
168. Von Bekesy, G., Neural Volleys and the Similarity between Some Sensations Produced by Tones and by Skin Vibrations. J. Acoustical Soc. Am. 29:1059-1070, 1957.
169. Von Holst, E. and H. Mittelstaedt, Das Reafferenzprinzip. (Wechselsirkungen zwischen Zentralnervensystem un Peripherie). Z. Naturw., 37:464, 1950.

170. Walsh, E.G., The Perception of Rhythmically Repeated Linear Motion in the Horizontal Plane. Brit. J. Psychol. 53:439-445, 1962.
171. Wapner, S. and H.A. Witkin, The Role of Visual Factors in the Maintenance of Body-Balance. Am.J. Psychol., 385-408, 1950.
172. Webb Associates, NASA Life Sciences Data Book., Director of Aerospace Medicine, Contract R-89, NASA, 1962.
173. White, W.J., Acceleration and Vision, USAFWADC TR 58-333, Aero Medical Laboratory, Nov. 1958.

174. Whitsett, C.E., Jr., Some Dynamic Response Characteristics of Weightless Man. Technical Documentary Report No. AMRL-TDR-63-18, Wright-Patterson Air Force Base, Ohio, Apr., 1963.
175. Witkin, H.A., Further Studies of Perception of the Upright When the Direction of the Force Acting on the Body is Changed. J. Exp. Psychol. 43:9-20, 1952.
176. Witkin, H.A., The Nature and Importance of Individual Differences in Perception. J. Personality, 18:145-170, 1949.
177. Witkin, H.A., and S.E. Asch, Studies in Space Orientation. III. Perception of the Upright in the Absence of a Visual Field. J. Exp. Psychol., 38:603-614, 1948.
178. Witkin, H.A., and S.E. Asch, Studies in Space Orientation. IV. Further Experiments on Perception of the Upright with Displaced Visual Fields. J. Exp. Psychol., 38:762-782, 1948.
179. Witkin, H.A., and S. Wapner, Visual Factors in the Maintenance of Upright Posture. Am. J. Psychol. 63:31-50, 1950.
180. Woellner, R.C., The Perception of Vertical in the Presence of Increased Accelerative Forces. Bureau Med. & Surg., Research Project NM 17 01 11, Subtask 1, Report No. 45, 1957.
181. Woellner, R.C. and A. Graybiel, Counterrolling of the Eyes and its Dependence on the Magnitude of Gravitational or Inertial Force Acting Laterally on the Body. J. App. Physiol., 14: 632-634, 1959.
182. Woellner, R.C. and A. Graybiel, The Loss of Counterrolling of the Eyes in Three Persons Presumably without Functional Otolith Organs. Ann. Otol, Rhin. & Laryng., 69:1006-1012, 1960.
183. Worchel, P., The Role of the Vestibular Organs in Space Orientation. J. Exp. Psychol. 44:4-10, 1952.
184. Worchel, P., The Vestibular Organs in Space Orientation. Perceptual and Motor Skills, 5:164, 1955.

185. Ziebolz, H. and H.M. Paynter, Possibilities of a Two-Time Scale Computing System for Control and Simulation of Dynamic Systems. Proc. Nat. Electronic Conf., Vol. 9, February, 1954.
186. Ziegenruecker, G.H., and E.B. Magid, Short Time Human Tolerance to Sinusoidal Vibrations. USAF WADC TR 59-391, Aero Medical Laboratory, July, 1959.

Additional Reference:

187. Fogel, Lawrence J., Biotechnology: Concepts and Applications. "The Position- and Motion- Sensing Channel", pp. 145-165. Prentice-Hall, Inc., Englewood Cliffs, N.J., 1963.